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# Eastern Pacific Expeditions of the New York Zoological Society. XXXVIII. Intertidal Brachygnathous Crabs from the West Coast of Tropical America with Special Reference to Ecology.<sup>1</sup>

JOCELYN CRANE.

Research Zoologist, Department of Tropical Research,  
New York Zoological Society.

(Text-figures 1-3).

[This is the thirty-eighth of a series of papers dealing with the collections of the Eastern Pacific Expeditions of the New York Zoological Society made under the direction of Dr. William Beebe. The present paper is concerned principally with specimens taken on the Eastern Pacific Zaca Expedition (1937-1938); for general data, see *Zoologica*, Vol. XXIII, No. 14, pp. 278-298. A few were taken at Clarion I. on the Templeton Crocker Expedition (1936), and on subsequent trips to Panama and Ecuador made by the author in 1941 and 1944].

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## INTRODUCTION.

This paper consists of three parts. The first is an annotated list of species of intertidal brachygnathous crabs taken between Cape San Lucas, Lower California, and Guayaquil, Ecuador, between 1937 and 1944, with special reference to color in life and other field observations. Fifty-one species, comprising more than 2,000 specimens are recorded. These figures exclude 29 species of Ocypodidae, the reports of which have already been published. Except as noted below, the synonymy of Rathbun's monographs is accepted (1918, 1925, 1930). In the report, one new species (*Metapocarcinus concavatus*) is proposed. One species is reduced to subspecific status (*Thoe sulcata panamensis*). *Mithrax areolatus* is considered a synonym of *M. denticulatus*, and *Xanthodius hebes* of *X. sternberghii*.

The second part discusses the habitats of these species and of the expeditions' ocypodids.

The paper concludes with some general remarks on the field observations.

In this report, the term "intertidal crabs" is used to embrace those species occurring typically in a habitat which is under tidal influence, so that the crabs are more or less amphibious. Rocky, sandy and muddy niches are included, as are those subject to moistening by waters of various degrees of salinity.

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TEXT-FIG. 1. Shore collecting stations of the Eastern Pacific Expeditions of the New York Zoological Society.

In the delimitation, for ecological purposes, of such a group of species, various difficulties are naturally encountered, although in most cases there is no question as to the propriety of including a given zone or species. The only ecologically questionable zone treated is that of *Pocillopora* coral; it is included because most of the species inhabiting it occur also in definitely tidal zones, rather than in deeper waters. In regard to taxonomic groups, it was finally decided to exclude the following: all the Portunidae, Goneplacidae and Pinnotheridae, in spite of the fact that species of these families were occasionally taken in tidepools, coral, or in high-tide seines; the

Gecarcinidae, although they occur on the fringes of both beach and mangrove areas; several *Sesarma* which proved as typically fresh-water inhabitants as the Potamonidae, although they also occurred in the upper reaches of tidal streams; and all *Plagusia*, which, although rarely found in tidepools, are characteristically oceanic.

The following papers have already been published on the brachyuran crabs of the Eastern Pacific Expeditions of the New York Zoological Society: Glassell, 1936; Crane, 1937.1, 1937.2, 1940, 1941.1, 1941.2, 1943, 1944 (see "References Cited"). Those papers still to appear include reports on ocyropods



from Ecuador, on the non-tidal brachygnaths of the Eastern Pacific Zaca Expedition (1937-1938), and on the non-brachygnathous crabs collected on the same trip.

In the following "Annotated List of Species," references are given to the type description, to Rathbun's monograph, and to records which have appeared since the monograph. The zone numbers following the habitat description refer to the various types of habitat described in the section beginning on p. 86.

I wish to express my thanks to Dr. Waldo L. Schmitt of the United States National Museum and to Dr. John Garth and other members of the staff of the Hancock Research Foundation of the University of Southern California for their friendly cooperation in giving me access to comparison material in their respective collections.

## ANNOTATED LIST OF SPECIES.

### FAMILY MAJIDAE.

*Eucinotops panamensis* Rathbun, 1923, p. 73; 1925, p. 87. 19 specimens from Costa Rica (Port Parker, Piedra Blanca, Uvita) and Panama (Honda). Usually in tidepools, rarely under low-tide stones (Zones 4, 3). Eggs in Jan., Mar. (C.R.).

Color of 16 specimens from Piedra Blanca found in single small patch of fine green algae: Carapace and ambulatories forest green above; manus mottled forest green and greenish-yellow; dactyls white; underparts of body entirely bluish-white striped transversely with broken lines of purplish-blue; underside of ambulatories forest green; bits of weed and sand grains attached to carapace and chelipeds; eggs orange. Specimens from other localities also decorated with weed.

Range: Gulf of California to Panama.

*Acanthonyx petiveril* Milne Edwards, 1834, p. 343; Rathbun, 1925, p. 142; Boone, 1927, p. 137; Hult, 1938, p. 11; Garth, 1946, p. 376. 23 specimens from Nicaragua (Corinto), and Costa Rica (Piedra Blanca). Among elongate algae growing either in tidepools or, rarely, on exposed, surf-beaten rocks (Zones 4, 1). Also occasionally found below low-tide level. Eggs in Jan., Feb. (Nic., C. R.).

Color ranges from bright lettuce green through ochre and brown to deep maroon, depending entirely upon color of surrounding algae; in one pool, the crab was found on six or eight kinds of algae, all of different colors, so that extremes of variation were found on crabs living within 6 inches of one another; the greenest ones lived on a kind of smooth sea lettuce, and were smoother, with fewer tubercles, than the others. This variation in tubercles is well known, but the matching of smoothness and color to background has apparently not been recorded. In

relatively few examples, long flags of weed particles were attached to rostrum. One crab, ochre-colored, had several pale, central, bryozoan-like markings. Eggs orange.

Range: Southern Florida to Brazil; Mexico to Chile; Galápagos.

*Pelia pacifica* A. Milne Edwards, 1875, p. 73; Rathbun, 1925, p. 283. 26 specimens from Mexico (Acapulco), Nicaragua (Corinto), Costa Rica (Jasper I., Uvita) and Panama (Honda). Clinging to underside of low-tide stones, in tidepools, and in *Pocillopora* coral; once on orange seafan (Zones 3, 4, 5). Eggs in Jan., Feb., Mar. (Nic., C. R.).

Color at Uvita, on undersides of sponge- and algae-grown stones: Bluish-gray above, pile ochraceous yellow. Chelipeds: merus and manus translucent buff peppered with black; carpus and chelae flame scarlet. Underparts buffy green. Eggs orange. General color in tidepools at Corinto: dark red. Many specimens from various localities were well covered with hydroids (anteriorly only), sponges, algae and sand grains.

Range: Manzanillo, Mexico, to Panama.

*Thoe sulcata sulcata* Stimpson, 1860, p. 177; Rathbun, 1925, p. 349; Crane, 1937, p. 59. 28 specimens from Mexico (Clarion I., Chamela, Tenacatita, Sihuatenejo). In tidepools and *Pocillopora* coral (Zones 4, 5). Eggs in Nov., Dec. (mainland), May (Clarion). Text-fig. 2B.

Range: Gulf of California and west coast of Mexico to Oaxaca.

*Thoe sulcata panamensis* Nobili, subsp. nov.

(Text-fig. 2A).

Synonymy: *Thoe panamensis* Nobili, 1901, p. 30; Rathbun, 1925, p. 351 and syn.; Finnegan, 1931, p. 624.

67 specimens from Nicaragua (Cardon I., at Corinto), Costa Rica (Port Parker, Culebra, Piedra Blanca, Jasper I., Uvita) and Panama (Honda). Undersides of rocks and stones at extreme low-tide levels, in tidepools and in *Pocillopora* coral (Zones 3, 4, 5). Eggs in Jan., Feb., Mar. (C. R. and Pan.).

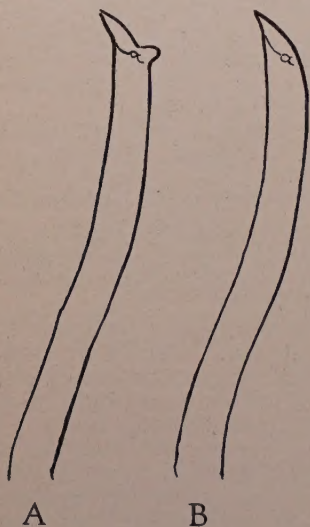
The two species, *sulcata*, ranging south to Oaxaca, and *panamensis*, known previously only from the Bay of Panama, have heretofore been distinguished by two characters: first, by the development of the outer row of excavations on the arm, which are well developed in *sulcata* and obsolete or obsolescent in *panamensis*, and second, by the spinulation of the upper margin of the ambulatory merus, which is strongly spinous in *sulcata* and only obscurely so in *panamensis*. Briefly, therefore, the northern form is more spinous and eroded.

Rathbun's suggestion that *panamensis* may perhaps not be specifically distinct is shown to be true by the present extensive series. Because of the variation in the development of both the excavations and spines



in northern and southern forms, there seems no valid specific distinction. Were it not for a sharp change in a detail of the abdominal appendage at about the latitude of Tehuantepec, the species should even be regarded as monotypic, although showing a tendency to form a geographical cline.

Even in the most northern, typical *sulcata*, the outer row of pits on the arm is completely developed only in the largest males, less so in the largest females; in other examples, only two or three outer excavations are present and these are confined to the distal part of the arm. In some examples from Nicaragua, on the other hand, the pits are so well developed that the specimens could almost be referred to *sulcata*, were it not that the spinulation on the ambulatory meri is very weak. In a series from Port Parker, Costa Rica, the pits are so variable that they are taxonomically useless, while there are traces of spinulation on the legs. In specimens from Jasper I., C. R., some examples have spines almost as strong as in typical northern *sulcata*; the rest of the Jasper series are typical *panamensis*.



TEXT-FIG. 2. Right abdominal appendages in subspecies of *Thoe sulcata*, postero-lateral views of distal halves. A. *T. sulcata panamensis*. B. *T. sulcata s.*

The only sharp distinction in any is the form of the abdominal appendage. In all specimens taken north of the Gulf of Tehuantepec, there is no subterminal spur on the anterior inner surface; from Nicaragua south a very distinct spur invariably occurs. (We have no specimens from the intermediate region). The spur does not decrease gradually in size or prominence, from south northward, as would be the case in a cline;

the change is complete and abrupt. Additional specimens from the Cape San Lucas region, examined in the Hancock collection show the same distinction in contrast to southern forms as do those from middle Mexico. It is on this basis that the relegation of *panamensis* to the status of subspecies is proposed.

Both subspecies are similar in color and habit. They are clingers, and are especially to be found among yellow sponges growing on stones and dead corals well covered with these and other animal and vegetable growths, at extreme low-tide levels, in tide pools and in *Pocillopora* coral. They are usually well decorated with the shells of *Spirorbis*-like polychaetes, bryozoans and other growths. Their basic color (Costa Rica) is dull yellowish-brown, except for manus of chelipeds which is pinkish, and the dactyls which range from deep rose to bright orange, shading distally to white. All underparts white. Females are usually more brown, less yellow, than males; young (around 4 mm.) paler yellow than adults with manus violet, not pink; chelae even at this stage are bright orange.

Range: Corinto, Nicaragua, to Panama.

***Herbstia tumida*** (Stimpson, 1871, p. 95) Rathbun, 1925, p. 299; Finnegan, 1931, p. 623; Crane, 1937, p. 59. 1 immature female from Panama (Honda). Previously known only from Mexico. On under side of stone at extreme low-tide level (Zone 3). Specimen compared with example in Hancock Foundation which was identified by Rathbun, and with other southern material in the same institution, which has not yet been recorded.

***Pitho sexdentata*** Bell, 1835, p. 172; Rathbun, 1925, p. 367; Sivertsen, 1933, p. 11; Crane, 1937, p. 60; Garth, 1946, p. 387. specimen from Costa Rica (Port Parker). Previously known from Cape San Lucas, the Gulf of California, Ecuador and the Galápagos. On underside of stone at extreme low-tide level (Zone 3).

***Anaptychus cornutus*** Stimpson, 1860, p. 184 (56); Rathbun, 1925, p. 378. 40 specimens from Mexico (Chamela, Sihuatenejo), Costa Rica (Port Parker, Culebra, Piedra Blanca, Jasper I., Ballenas, Uvita) and Panama (Honda). Under side of stones at extreme low-tide level, in tidepools and in *Pocillopora* coral (Zones 3, 4, 5). Eggs in Nov. (Mex.), Jan., Feb., Mar. (C. R., Pan.)

Color at Chamela, in tidepool: Olive green overgrown with white bryozoans, green and purple sponges and algae. Eggs purplish black (ready to hatch). Specimens from all localities typically covered with calcareous algae, sponges, hydroids, bryozoans, serpulids, barnacles and sand grains.

The number of tubercles or lobes on the central portion of the posterior crest varies from six to eight; often the lobes are so low



that the crests appear practically entire. Antero-lateral margins with lobes very variable, some almost as spinous as in *Mithrax*. Rostrum and pre-ocular spines are apt to be broken.

Range: Gulf of California to Panama.

*Mithrax denticulatus* Bell, 1835, p. 172; Rathbun, 1925, p. 428; Boone, 1927, p. 161; Garth, 1946, p. 395.

Synonymy: *Mithrax areolatus* Lockington, 18876, p. 71 (9); Rathbun, 1925, p. 433; Crane, 1937, p. 48.

86 specimens from Mexico (Chamela, Bihuatenejo, Guatulco, Tangola-Tangola), Costa Rica (Port Parker, Culebra, Piedra Blanca, Uvita) and Panama (Honda). On undersides of large stones at extreme low-tide levels, in tidepools among short weed and in *Pocillopora* coral (Zones 3, 4, 5). Eggs in Nov., Dec. (Mex.); Jan., Feb., Mar. (C. R., Pan.).

Color variable, but in general olive green to olive brown above, sometimes mottled, with hairs and underparts lighter. Notes from various localities indicate this variability: Chamela tidepools: Greenish with dark brown mottlings anteriorly. Port Parker coral: Carapace mottled chocolate brown and dull olive green; eyes chocolate brown; chelipeds and legs like carapace; hairs olive; distal half of chelae flesh pink; sternum and maxillipeds plain olive; abdomen white with joints brownish; underside of ambulatories greenish-white. Piedra Blanca, tidepools and undersides of rocks at extreme low-tide level: Entirely olive green to olive brown above, with hairs yellowish-brown; underparts buffy or greenish-white with joints of merus of cheliped bright orange; joints of ambulatories yellowish; chelae dark green tipped with cream. Uvita coral: Like above, but upper side plain dark olive with branchial sulcae white; young (ca. 4 mm. long) more light brown than olive. In other localities young were like adults. All eggs purple. When groups of living specimens were examined, in trays, all clung to one another in a ball, in lieu of weed.

*M. areolatus* Lockington should be synonymized with *M. denticulatus*. Our specimens vary in relative width, giving proportions intermediate between the diagnostic characters for the two species. Also, if Lockington and Kingsley omitted spines in their breadth measurements, the proportions of *areolatus* would approach those of *denticulatus*. Finally, the equal or unequal advance of the antennal articles is not a reliable character, since in the present series variation occurs on two sides of the same individual, and in different specimens from the same locality.

Range: San Diego, California, to Ecuador.

*Mithrax orcutti* Rathbun, 1925, p. 397. 1

immature male from Nicaragua (Corinto). Clinging to ochre weed in tidepool, and matching it perfectly in color (Zone 4).

Range: Mazatlan, Mexico, to Panama.

*Mithrax pygmaeus* Bell, 1835, p. 172; Rathbun, 1925, p. 406; Finnegan, 1931, p. 624; Hult, 1938, p. 12; Garth, 1946, p. 391. 4 specimens from Costa Rica (Port Parker, Culebra). First records north of Panama. In *Pocillopora* coral (Zone 5). A few other specimens, dredged in shallow water, will be recorded in a future report.

Some examples tend to have the front subtruncate instead of rounded. The spines, counting tubercles, may number 7 instead of 6.

Range: Costa Rica, Panama, Galápagos, Ecuador.

*Teleophrys cristulipes* Stimpson, 1860, p. 190 (62); Rathbun, 1925, p. 441; Finnegan, 1931, p. 625; Crane, 1937, p. 61; Glassell, 1934, p. 453; Schmitt, 1939, p. 25; Garth, 1946, p. 396.

Synonymy: *T. diana* Boone, 1927, p. 162; Sivertsen, 1934, p. 13; Hult, 1938, p. 12.

*T. tumidus* Rathbun, 1925, p. 442 (part.: the Galápagos specimen); Boone, 1927, p. 166.

99 specimens from Mexico (Chamela, Guatulco, Clarion I.), Costa Rica (Port Parker, Culebra, Jasper I., Uvita) and Colombia (Gorgona I.). Always in *Pocillopora* coral except for one specimen in a tidepool and another at low-tide level in dead pearl oyster (Zones 5, 4, 3).

Color in general olivaceous. Almost all the crabs were naked except, rarely, for two or three tiny *Spirorbis* encrustations. One specimen was decorated with a few algae.

Garth (1946, p. 399 ff.) has clarified the distinctions between *T. cristulipes* and the Peruvian *T. tumidus*, and commented on the variation in the two species. Our own series support his conclusions: In our two Gorgona examples, the crestiness and the anterior tooth are more strongly developed than in more northern specimens, and there is a crest similar to that of *tumidus* on the posterior part of the propodus. Comparison with specimens of both *tumidus* and *cristulipes* in the Hancock collections, however, leaves no doubt that the Gorgona specimens show only normal variation. Both Garth and Finnegan (1931, p. 625) noted that specimens of *cristulipes* cracked from coral had the legs more cristate and the spines of the anterolateral margins better developed than those from shore. In our examples great variation is shown even though almost all were taken from submerged corals. Even series of similar size from the same coral-head show considerable range. In the type series of *T. diana* Boone from the Galápagos, taken from corals in 15 feet of water, the specimens are all relatively smooth.



Range: Lower California to Colombia; Galápagos.

*Microphrys platysoma* (Simpson, 1860, p. 180); Rathbun, 1925, p. 497; Crane, 1937, p. 63; Garth, 1946, p. 405. 7 specimens from Mexico (Clarion I.), Costa Rica (Port Parker, Uvita) and Panama (Honda). Under stones at low-tide level, in tidepools and in *Pocillopora* coral (Zones 3, 4, 5). Specimens usually completely covered with vegetable and animal growth.

Range: Lower California to Ecuador; Galápagos.

#### FAMILY PARTHENOPIDAE.

*Daldorfia garthi* Glassell, 1940, p. 68 and syn.; Garth, 1946, p. 412. 1 specimen from Costa Rica (Port Parker), a large, worn male, taken under a rock at extreme low-tide level (Zone 3). When this specimen was compared with material in the Hancock collections from various localities, the following differences from the type description were found to be only normal variation: Postero-lateral and posterior margins are not straight; spines on antero-lateral margin are smaller and simpler; meri of ambulatories are practically smooth, lacking spines on dorsal (anterior) side; the abdomen is sculptured somewhat differently.

Range: Cape San Lucas, Lower California, to Colombia; Galápagos.

#### FAMILY XANTHIDAE.

*Carpilodes cinctimanus* (White, 1847, p. 336); Rathbun, 1930, p. 242; Crane, 1937, p. 69; Garth, 1946, p. 427. 15 specimens from Mexico (Clarion I., Guatulco), Costa Rica (Port Parker, Culebra, Jasper I.). In *Pocillopora* coral (Zone 5). One ovigerous female in Feb. from Jasper I.

Color as given by Rathbun, Garth and Crane, except that general color is often deep scarlet instead of light red, orange, or dragon's blood red. Black band of male manus never developed in specimens less than 9 mm. long; also lacking in one male of 12.5 mm. Smallest examples in our mainland series (around 5 mm.) are completely white above and below except for scarlet orange chelipeds and ambulatories. Cf. Garth's Galápagos growth series.

Range: Arena Bank in Gulf of California to Costa Rica; Galápagos; South Sea Islands; Japan and Australia to Gulf of Aden.

*Actaea dovii* Stimpson, 1871, p. 104; Boone, 1927, p. 203; Rathbun, 1930, p. 254; Finnegan, 1931, p. 632; Sivertsen, 1933, p. 15; Schmitt, 1939, p. 25; Garth, 1946, p. 431. 77 specimens from Costa Rica (Port Parker, Culebra, Piedra Blanca, Jasper I., Uvita), Panama (Honda, Pearl Ids.). In tidepools (among weed and under stones) and in *Pocillopora* coral (Zones 4, 5). Eggs in Jan. and Mar. (C. R., Pan.).

Varying considerably in color, but eye always bright red. Adults: carapace and legs ranging from dull orange through brown to plum color; underparts white except pterygostomian region, merus of third maxilliped, and manus and dactyl of ambulatories which are lavender; chelae dark brown tipped with buff; pile of carapace, legs and edges of abdomen ochre. Young (around 5 mm.) always with three dark red longitudinal bands alternating with two white bands, the latter being broadest in the very young. Sometimes the three red bands are broken irregularly, so that a checkerboard-like carapace results; legs all banded with dark red and white; nodules in dark stripes raspberry red, others white. One half-grown specimen was dull orange above with purplish legs. The color recorded by Rathbun of a Galápagos specimen ("eleven orange-red stripes extending backward from frontal and antero-lateral margins and converge posteriorly") and figured by Garth was not seen on any of the present specimens. Eggs dark purple.

The crabs always remain well concealed. Bits of shell and sand cling to the pile of the carapace and help make them inconspicuous. As they lie perfectly quiet in crevices in the coral and in tidepools, only their gleaming eyes, ranging in color from brilliant scarlet to vermilion, are visible.

Range: El Salvador to Ecuador; Galápagos.

*Actaea sulcata* Stimpson, 1860, p. 203; Rathbun, 1930, p. 259; Finnegan, 1931, p. 632; Crane, 1937, p. 69; Garth, 1946, p. 434. 8 specimens from Mexico (Clarion I., Tenacatita, Sihuatenejo, Guatulco) and Costa Rica (Port Parker, Jasper I.). In *Pocillopora* coral; once under tidepool rocks (Zones 5, 4). One ovigerous female at Sihuatenejo in Nov.

Color at Tenacatita, whitish with tubercles rose red except around eyes where they are white. Cf. color of Gulf of California specimens which were orange-red and orange-red mottled with white (Crane 1937), and Galápagos specimens which were "neutral red with bluish tinge" with posterior median nodules "yellowish white" (Garth, 1946).

Range: Arena Bank, Gulf of California to Colombia; Galápagos.

*Daira americana* Stimpson, 1860, p. 212 (84); Rathbun, 1930, p. 268; Crane, 1937, p. 70; Hult, 1938, p. 12; Garth, 1946, p. 439. 40 specimens taken from Mexico (Clarion I., Chamela), Costa Rica (Port Parker, Culebra, Uvita), Panama (Honda). In *Pocillopora* coral; sometimes under low-tide stones (Zones 5, 3). Eggs in Jan., Mar. (C. R.).

Color as in Crane, 1937, but abdomen often tinged with purple instead of carmine.

Food: 6 stomachs from Port Parker.



square bits of flat, brown algae, not macerated.

Range: Lower California to Ecuador; Galápagos.

*Medaeus spinulifer* (Rathbun, 1898, p. 585); 1930, p. 276; Finnegan, 1931, p. 643; Garth, 1946, p. 443. 2 specimens from Costa Rica (Jasper I.). In *Pocillopora* coral (Zone 5). Also occurs in deeper water.

Range: Cape San Lucas, Lower California, to Costa Rica; Galápagos.

*Cycloxanthops vittatus* (Stimpson, 1860, p. 206 (78)); Boone, 1927, p. 197; Rathbun, 1930, p. 291; Sivertsen, 1933, p. 15. Garth, 1946, p. 445. 8 specimens from Mexico (Guatulco, Tangola - Tangola) and Costa Rica (Port Parker). Under rocks at extreme low-tide levels and in *Pocillopora* coral (Zones 3, 5).

Color variable: Port Parker: one specimen uniformly pale tan; one white with a few black spots, a scarlet spot on cardiac region and one on each carpus of chelipeds. Fingers dark brown. Tangola-Tangola: Carapace and legs grayish-brown; chelae black; underside pale except abdomen, which is like carapace with a white line down middle. Eggs dark brown.

Range: Cape San Lucas, Lower California, Mexico to Panama; Galápagos.

*Leptodius taboganus* Rathbun, 1912, p. 3; 1930, p. 304. 62 specimens from Costa Rica (Port Parker, Piedra Blanca, Parida, Cedro L., Golfito), Panama (Honda) and Colombia (Gorgona I.). First records north of Panama. Under stones and rocks between tide levels (Zones 2, 3).

General color greenish with underparts lighter. Cedro I.: Carapace and chelipeds dark olive green; legs light olive, spotted with white; dactyls dark brown; underparts pale olive gray; eggs black. Golfito: Greenish-gray to greenish-brown above, speckled with dark blue; usually also a few white spots on carapace; chelae blue black to pale brown; lower half of manus buffy white to light brown. All underparts blue marbled with white except pterygostomian region, which is buffy white. Cf. Schmitt's notes in Rathbun, 1930, on Ecuador specimens ("sage greenish in general, mottled with some lighter traces of pea green.").

Range: Costa Rica to Ecuador.

*Xanthodius sternberghii* Stimpson, 1859, p. 52; Rathbun, 1930, p. 311 and synonymy. Synonymy: *Xanthodius hebes* Stimpson, 1860, p. 208 (80); Rathbun, 1930, p. 313 and synonymy.

165 specimens from Mexico (Sihuatenejo, Puerto Angeles, Guatulco, Tangola), Nicaragua (Corinto, San Juan del Sur), Costa Rica (Port Parker, Piedra Blanca, Cedro, Ballenas, Uvita, Golfito), Panama (Honda) and Colombia (Gorgona). Hundreds more seen but not collected. Under stones between

tide levels on moderately protected shores; more rarely, in tidepools (Zones 2, 3, 4). Eggs in Dec. (southern Mexico, Nicaragua), Jan. (Nic., C. R.), Feb., Mar. (C. R.), Apr. (Pan., Col.).

The color varies irrespective of sex or size, from black through dark greens, grays and brown to buff and white, blending with the substratum, often speckled or blotched. A well-marked phase is dark with median pale stripe; this form occurs sporadically in varying numbers in different populations, and appears irrespective of substratum color. Ambulatories often banded distally with purple and yellow. The faithful matching of their environment, plus their habit of sheltering under stones, must give these crabs excellent protection, whether they are quiescent during low tide or actively feeding under water. When the background is homogeneous in color, the individuals of the population usually vary little, except for the usual scattering of often conspicuous individuals with a median white stripe. Where the background varies because of different colored pebbles, for instance, individuals within a radius of a few feet can be found to match every pebble in the habitat, from whitest to darkest.

The following field notes made in various localities indicate the range of variation within typical populations: *Guatulco*: majority ranging from pure white with a few brown spots through brown and gray speckled mixtures to black marked with gray; a few completely dark gray above, chelae black, and legs purple with joints and dactyls yellow. *Tangola-Tangola*: Carapace and chelipeds of large male olive green finely stippled with dark brown; ambulatories the same, with merus-carpal joint bright yellow, manus violet, dactyl straw; chelae grayish-brown; entire ventral surface except manus and dactyl of ambulatories white. Ovigerous female similar, but all of ambulatories violet except merus joint and dactyl as above, and abdomen speckled with olive on white. Carapaces of other females close by: (1) black, mottled in median region with pure white; (2) black with fine white mottlings; (3) white with black marblings; (4) white marbled with chocolate; ambulatories of all these phases more or less violet, with merus joints and dactyls yellow. *Isla Cardon, Corinto*: Population in relatively exposed position, mostly among dark rocks; majority dark brown, but when the stones are on sandy substratum, crabs often with one or two median streaks or lines of spots, pure white, down middle of carapace, especially on gastric region. Individuals also marbled greenish-buff with darker green, matching sand; this phase was especially common in the young of this population; chelae of young very pale brownish. Dark-



est crabs in general occurred among dark rocks of the more exposed tidepools. *Culebra* (seen, but not collected): great majority matching dark volcanic sand which forms substratum for stones; crabs of lighter shades occurring only in less protected regions, where they were rare, matching the tossed-up, water-worn coral. *Piedra Blanca*: 7 mm. male (none taken smaller than this); carapace bluish-violet except for white postero-lateral margin; legs dark. 10 mm. male: grayish-white except for ambulatories which have carpus lavender and dactyl straw. In both young and adults the eye-stalks always matched perfectly the circumorbital region of carapace. *Cedro I.*: Carapace of majority green-black, but those with median white stripe more than usually common. Eggs black.

In structure as well as in color these crabs proved to be exceedingly variable, as is to be expected with a widely distributed, successful species. Although they were the most abundant under-stone brachyurans on semi-protected shores the entire length of western Central America, the present report is the first to be published on a series gathered from many localities. Examination of these specimens and comparison with as yet unrecorded Hancock expedition examples from the same and more northern localities make it apparent that *Xanthodius hebes*, recorded from Lower California, and *X. sternberghii* from Cape San Lucas and from Panama to Peru, are not distinct species. *X. hebes* has been distinguished by: (1) the thicker, blunt, antero-lateral margin; (2) by the edge of the front being invisible, not visible in a dorsal view; (3) by the narrower carapace (in which the length is contained  $1\frac{1}{2}$  instead of  $1\frac{3}{4}$  times in the breadth) and in the broader abdomen. It is perfectly true that some individuals show these differences very distinctly, and in these, in addition, correlated with the shape of the abdomen, the abdominal appendage of the adult male is shorter, broader and more curved in *hebes* than in *sternberghii*. (A constant, corresponding difference in the female genital passage could not, however, be discerned). It is also true that the extreme *sternberghii* form appears less often in our collections made in Mexico than farther south. However, no basis whatever appears for recognizing even a geographical cline, much less a subspecies or species. In the more southern localities some populations were composed altogether of one form, others of the second, and still others, the majority, showed a preponderance of recognizable *hebes*, a few indecisive examples, and still fewer *sternberghii*. The width of the carapace was found to be the most variable character of all. Since the remaining characters cannot be accurately measured, but

depend on ocular comparison, they cannot be scientifically tabulated. However, in counts made with all the specimens spread out and visible at once, on three successive days, the following average totals were obtained: *hebes* form 80, dubious 44, *sternberghii* form 41. Clear-cut *hebes* and *sternberghii* forms were rare. Age and sex appear to have nothing to do with the appearance of the form and color variations do not link up with the morphological differences. Unfortunately, at the time the collections were made the difficulties of the taxonomy were not recognized, so that populations taken in slightly different niches in the same bay—for example, from portions of the shore differing in water salinity—were not kept separate. From the field notes, however, it appears possible that the *hebes* form, which owes its morphological characteristics basically to heavier deposits of mineral, represents merely a non-genetic response to environmental conditions. The population containing the largest individuals of the entire collection consisted almost wholly of pure *hebes*-type individuals, and was taken at Cardon Island, a relatively exposed locality close to the open sea near Corinto, Nicaragua; the large size of these specimens is another example of the frequently observed phenomenon that in invertebrates large size and high salinity are linked.

**Behavior:** Their observed behavior may be divided into two distinct parts: the quiescent period, when the tide is out, and the active period of feeding during high water. Their usual habitat at low tide is under stones, where they occur from the highest to the lowest tidemarks.

During low water, they are among the least mobile of the xanthids, and when first exposed or disturbed, remain motionless, with the betraying, non-pebble-like legs curled under them. The second defense reaction, among adult and sub-adult males, is the typical crab threat posture, with wide-spread chelicerae and gaping chelae. Females and young never threaten, but maintain the curled-up possum-playing position often for many minutes, even when turned on their backs.

When covered by water and undisturbed, they move about in the open, even in bright sunlight, feeding on algae. Always, however, they remain near the refuge of a stone or crevice.

When observed in tidepools, their feeding habits can be studied in detail. The algae is picked with the minor cheliped, the major being used for bracing and balancing. This balancing is doubtless necessary because most of the crab's weight is anteriorly placed, in the broad front and massive chelipeds; hence feeding with both



claws would be impossible, in contrast to *Pachygrapsus*, which has small chelipeds, and long legs holding up a moderate carapace and which feeds using both claws alternately. In *Xanthodius* the first and second ambulatories do most of the work in ordinary sidewise walking, the third helps, and the fourth, as well as both chelipeds, are suspended and do not touch the substratum except in climbing. The crabs feed at remarkable angles, often upsidedown, or standing on their hind legs and reaching far above with their minor chelae for especially rich patches of algae. Although they feed only a few seconds in one spot, then move on an inch or two, most individuals remain within a radius of about six inches. At Corinto, where observation conditions were especially favorable, they paid no attention to the little sand-colored blennies, which passed within an inch of them, but seemed to avoid the scarlet-legged hermit crabs, which fed on the same algae. On the other hand, the two forms occasionally fed within an inch of each other. Often, in several localities a single grown male was found under a damp rock or in a pool with two or three ovigerous females and one or more young. None was ever seen feeding out of water, or crawling on exposed rocks, yet they were found almost to extreme high tidemarks, as well as near low tide. At Cardon Island, Corinto, where night observations on tidepool animals were made, not a single *Xanthodius* was seen after dark; if they are exclusively diurnal, the feeding periods for the highest crabs must be very brief, unless migrations are made.

Range: Lower California to Peru.

*Xanthodius stimpsoni* (A. Milne-Edwards, 1879, p. 252); Rathbun, 1930, p. 315. 45 specimens from Mexico (Guatulco) and Costa Rica (Port Parker, Piedra Blanca, Uvita). Usually under encrusted stones exposed near low-tide level; rarely in tidepools and *Pocillopora* coral (Zones 3, 4, 5). Eggs in Dec. (Mex.), Jan., Mar. (C. R.).

Color very variable. Immediate environment usually consists of stones encrusted with varicolored animal life, with which crab in general blends. Adults, above, usually entirely black, greenish-black or dark gray mottled with gray, light green or cream, but may be dark brown with antero-lateral and frontal borders and all ambulatories pinkish-tan; chelipeds may be contrastingly pale or, occasionally, entire crab is buffy. Underparts usually pale, sometimes mottled. Very young crabs tend to be paler than adults. A single young was pinkish-tan with a median longitudinal white stripe like that often found in *sternberghii*; chelipeds chocolate brown; ambulatories pinkish-tan.

Although these crabs feign death when

disturbed, they rouse and attempt to escape more easily than do *sternberghii*. Usually they are never exposed more than one-half hour at each low tide.

Young crabs are rougher than old ones.

Range: Mouth of Gulf of California to Ecuador.

*Lophoxanthus lamellipes* (Stimpson, 1860, p. 205 (77)); Rathbun, 1930, p. 317. Garth, 1946, p. 451. 65 specimens from Mexico (Chamela, Tangola-Tangola), Costa Rica (Port Parker, Piedra Blanca, Uvita); Panama (Honda); Colombia (Gorgona). Under stones exposed near low-tide level, in tidepools, and, rarely, in *Pocillopora* coral (Zones 3, 4, 5). Eggs in Dec. (Mex.), Jan., Feb., Mar. (C. R.), Mar. (Pan.).

Color very variable. Some taken in various localities, which agreed with Rathbun's description, being slate-colored with reddish-white chelipeds and antero-lateral margins; more were entirely different. Locality examples: Chamela tidepool: Dark gray except front and antero-lateral margins which were cream. Port Parker: Some entirely chestnut; some gray with white or yellowish antero-lateral rim; some all gray; chelae entirely black. Piedra Blanca: Carapace brown changing posteriorly to purplish-brown; frontal and antero-lateral margins buff; chelipeds plain white with black dactyls, their extreme tips light; ambulatories dull lavender with greenish-yellow dactyls; entire underparts (except those of white chelipeds) dull ochre. Uvita (under tidepool stones): color range about the same as at Port Parker and Piedra Blanca. Eggs always dark purple; dark brown when about to hatch. (Cf. also Garth, 1946).

Range: West coast of Mexico to Ecuador; Galápagos.

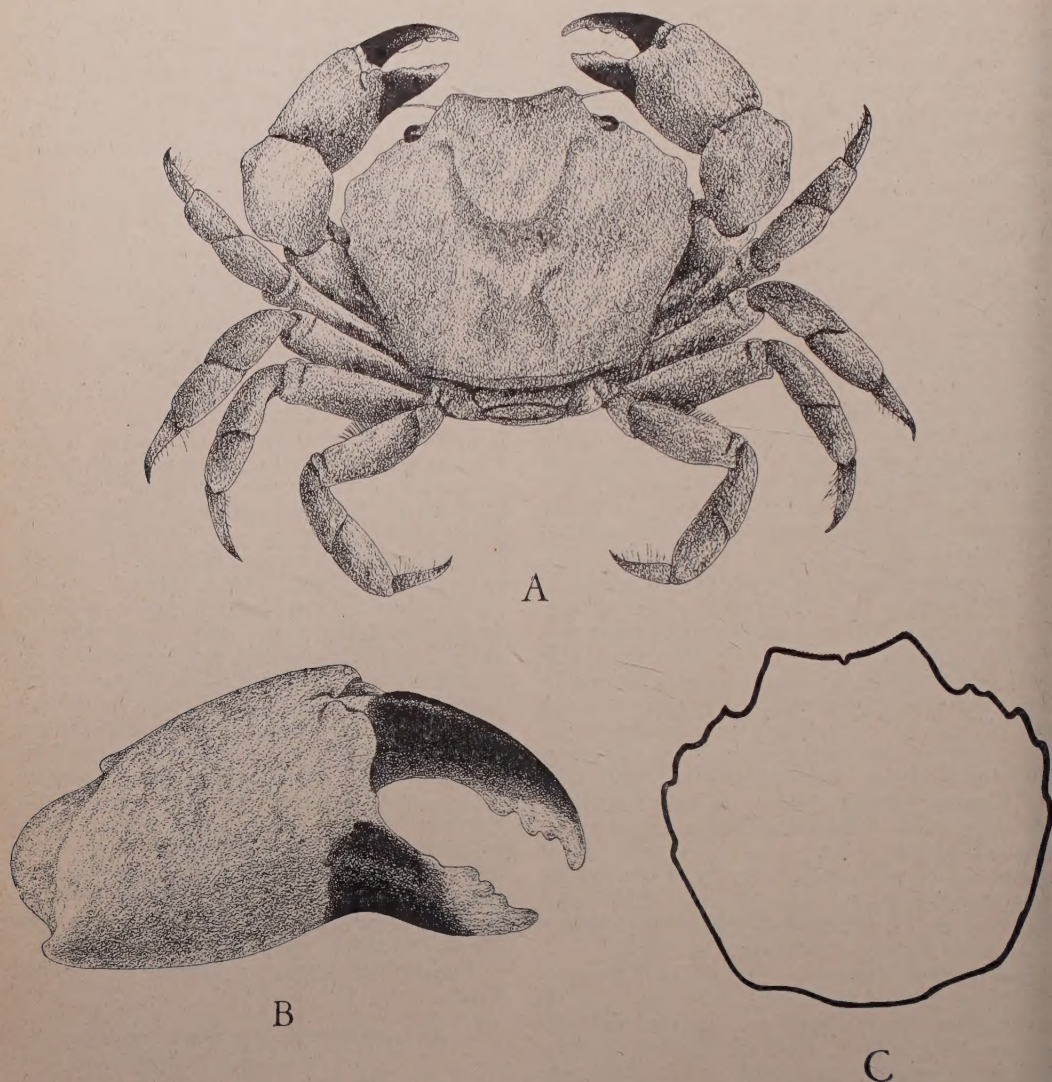
*Metapocarcinus concavatus* sp. nov.

(Text-fig. 3).

*Diagnosis*: Front concave, single-edged; no tooth at base of major dactyl.

*Description*: Carapace moderately convex in the antero-posterior axis, naked, the regions scarcely marked, very finely granulate. In the female there are four, short, transverse lines of granules across the anterior portion of the carapace: one pair on the antero-lateral regions, at the level of the third antero-lateral teeth, the other pair, slightly further forward and inward, on the lateral medial areolations. These granules are scarcely or not at all discernible in the males. Antero-lateral margin with five teeth or lobes, all distinctly granulate; the first, at orbital angle, small, narrow, blunt, the second broad, low, almost obsolete; the third broad and blunt, but the most conspicuous of the five; the fourth at widest part of carapace, smaller; and the fifth almost obsolete, at the point where





TEXT-FIG. 3. *Metapocarcinus concavatus*. **A.** holotype, dorsal view. **B.** major cheliped of holotype, external view. **C.** carapace outline of male paratype.

the marginal crest curves inward. The teeth tend to be noticeably asymmetrical on the two sides of each of the three crabs; in the juvenile male, the first and second lobes are better developed than in the others. Front very prominent, edge rather thick, but clearly only single-edged, granulate; it is concave, slightly sinuous, with a distinct median notch. Orbit with two closed fissures near outer upper edge; no noticeable lobe at middle of lower margin; inner lower angle a well-developed tooth which projects slightly beyond end of basal article of antenna; eyes filling orbit. Merus of outer maxillipeds about as broad as ischium, the distal edge transverse, slightly sinuous, the outer angle prominently pro-

duced, the inner distal edge broadly oblique and concave. Chelipeds and legs unarmed and naked, except for pile on dorsal (anterior) edges of ambulatory coxae, ischia and basal two-thirds of merus, and on ventral edges of feet. Chelipeds moderately unequal and massive, smooth except for microscopic granulations. Carpus with a blunt tooth at inner angle. Palms inflated; fingers gradually tapering, acuminate, with four blunt teeth in distal half of each chela; no tooth at base of prehensile edge of major dactyl; third to fifth segments of abdomen fused. Basal two-thirds of chelae dark, the dark color of pollex continued slightly on palm.

*Color in Life:* Male paratype from light



brown seaweed, in tidepool at Piedra Blanca: Carapace cream-colored; postero-lateral surfaces above bases of legs black, as recorded for *M. truncatus* by Stimpson (1860, p. 216 [88]). Chelipeds and ambulatories chocolate brown, except for pale dactyls; chelae brownish-black, except for tips which are pale. Underparts pale buffy brown. After nine years in alcohol, all of the color, except that of the chelae, has faded to creamy white.

*Measurements in mm.*: Male holotype length 5.6, breadth 6.1; female paratype, length 6, breadth 6.7, male paratype, length 4.8, breadth 5.2.

*Range*: The three known specimens were taken from Fumarole Shore, El Salvador (northern) side of Gulf of Fonseca and from Piedra Blanca, Costa Rica.

*Habitat*: The male paratype was in a brown, sargassum-like weed. Only this single specimen was taken in more than six carefully examined pailsful from the same tide-pool (Zone 4).

*Discussion*: The proposed new species differs from *Metapocarcinus truncatus* Stimpson, 1860, as follows:—

1. The front is angularly concave and slightly sinuous, not truncate.
2. The lateral teeth are somewhat less obscure, particularly the third which is well developed.
3. The front is not double-edged.
4. There is no shallow lobe at the middle of the lower margin.
5. The basal antennal article does not reach quite as far forward as the inner suborbital tooth.
6. The merus of the outer maxillipeds is scarcely or not at all narrower than the ischium, its distal margin not oblique, its distal outer angle quite sharply produced, not arcuate, the distal inner margin decidedly excavate instead of slightly notched.
7. The dorsal edges of coxae, ischia, and basal two-thirds of meri of all ambulatories are pilous.
8. There is no trace of a tooth at base of prehensile edge of dactyl of major cheliped.
9. Sixth abdominal segment of immature female not widening distally.

*Material*: Male holotype, Department of Tropical Research, No. 37,675, Fumarole Shore, northern side of Gulf of Fonseca, El Salvador, December, 1937; female paratype, No. 37,675a, same locality, same date as holotype; male paratype, No. 38,178, Piedra Blanca, Costa Rica, February 4, 1938. The types are deposited in the collections of the Department of Tropical Research, New York Zoological Society.

*Panopeus purpureus* Lockington 1876 (1877), p. 101 (7); Rathbun, 1930, p. 344. 14 specimens from Costa Rica (Culebra,

Ballenas, Golfito) and Ecuador (Puerto Bolivar). Eggs in late April at Puerto Bolivar. In stony mud on edges of mangrove swamps and open mudflats (Zones 6, 7).

*Range*: Mexico to Peru.

*Panopeus chilensis* Milne Edwards & Lucas, 1843, p. 16; Rathbun, 1930, p. 346. 21 specimens from Nicaragua (Corinto: Castenones lagoon) and Costa Rica (Culebra). Eggs in Jan. at Culebra. In stony mud on edge of lagoon (Zone 7).

*Range*: Mexico to Chile.

*Eurypanopeus planus* (Smith 1869, p. 283); Boone, 1927, p. 212, 1929, p. 571; Rathbun, 1930, p. 420. 121 specimens from Nicaragua (near Potosi in G. of Fonseca, Cardon I. at Corinto, San Juan del Sur); Costa Rica (Port Parker, Piedra Blanca, Cedro I., Uvita, Golfito), Panama (Honda), Colombia (Gorgona). Eggs in Jan. (Nic.), Mar. (C.R., Col.). Under stones at junction of sandy beaches and stony shores, where fairly large, but movable stones are strewn on sand between mean high and mean low tide (Zone 2). This is exactly the habitat occupied by *Uca panamensis*, rather than that of *Xanthodius sternberghii*, which is under stones at similar tide levels, but on a rocky, not sandy, substratum.

Color range in Central America agrees well with that recorded by Schmitt (in Rathbun) for Ecuadorian specimens. In our series, the light dots on the carapace were not always present, and, when there, were almost white, no matter what the ground color; they were invariably confined to posterior part of carapace. Very young crabs, 7 mm. or less in length, were usually plain brown with dead white chelipeds except for purple or brown white-tipped fingers. The purple cast of the chelipeds develops at various ages, the smallest in which it occurs measuring 7.5 mm. In this specimen both chilipeds were entirely light blue. No sexual color dimorphism was noted. Eggs black.

A single large male was occasionally found with a single ovigerous female under the same rock, or with two ovigerous females. Have never seen more than one adult made under one stone, although young ones may be present. When disturbed, adult males threaten with chelipeds and chelae widespread, holding them motionless, with the white underparts very conspicuous. They do not move for at least 10 minutes, even when the disturbing human being promptly goes far down the beach behind rocks and out of their sight. The females and young show no threatening action whatsoever, and merely lie quietly, wherever put. Fourteen stomachs contained the following: algae of various kinds, worm spicules, remains of a bright red worm, amphipods, unrecognizable organic detritus, and sand grains. Those speci-



mens killed toward the end of a low tide period were always empty. This fact, combined with their complete quiescence during low tide, makes it probable that they feed under water. They are always found half buried in a form under, or in the shelter of, a rock; it seems likely that they do not dig this deliberately since there is never any trace of claw marks, but that they settle into positions before the tide recedes and allow the draining sand to harden around them.

Five specimens (Nos. 3834, 3860 and 38164, from San Juan del Sur, Port Parker and Piedra Blanca) are infested with *Sacculina*.

Range: Gulf of California to Ecuador.

***Eurypanopeus transversus*** (Stimpson, 1860, p. 210 (82)); Rathbun, 1930, p. 407; Garth, 1946, p. 455. 111 specimens from Costa Rica (Port Parker, Culebra, Ballenas, Golfito) and Ecuador (Puerto Bolivar); many more seen than collected. Eggs in Jan., Mar., (C.R.); April (Ecuador). Under stones in the following localities: in gravelly mud, mud shores of bays and lagoons, among mangrove roots near high-tide mark, and on edges of open mud flats. (Zones 6, 7, 8).

Color: Ranging irrespective of locality from almost white to almost black, but most typical coloring as follows: Olive marbled with dark blue or black above; fingers black tipped with white; underparts olive buff.

Range: West coast of Mexico to Peru; Galápagos.

***Eurytium tristani*** Rathbun, 1906, p. 100; 1930, p. 425. 43 specimens from Nicaragua (Castenones lagoon at Corinto), Costa Rica (Culebra, Ballenas, Golfito), Ecuador (Puerto Bolivar). First record north of Costa Rica. Among mangroves and on edges of mudflats (Zones 6, 7).

General color dark brown; upper surface of chelipeds violet; of finger deep red.

Range: Nicaragua to Peru.

***Micropanope xantusii*** (Stimpson, 1871, p. 105 [15]); Rathbun, 1930, p. 438; Crane, 1937, p. 72; Garth, 1946, p. 457, and synonymy. 85 specimens from Mexico (Clarion I., Sihuatenejo, Acapulco) and Costa Rica (Port Parker, Culebra, Jasper I.). First records between Mexico and Galápagos. Eggs in Jan. at Port Parker. Always in *Pocillopora* coral (Zone 5), except for 3 young found at Port Parker in algae-covered stones among mangroves near low-tide level.

Color variable, but majority dark red mottled with lighter and darker. Sulci on major cheliped of adult males may be almost lacking.

Range: Clarion Island; Cape San Lucas, Lower California to Costa Rica; Galápagos.

***Menippe frontalis*** A. Milne Edwards, 1879, p. 264; Rathbun, 1930, p. 477. Synonymy: *Eurypanopeus purpureus*, Boone,

1929, p. 570. 6 specimens from El Salvador, in Gulf of Fonseca (Fumarole Beach and Concharita I.). First record north of Nicaragua. 1 female ovigerous (Dec.). Under dark volcanic stones (Zone 2).

General color brownish or grayish-purple, or purplish-brown (nearest in Ridgway: dark heliotrope slate); no trace of the red present in Rathbun's preserved specimen. Underparts buffy yellow. Mouthparts patched with violet. Upper outer half of manus veined with buffy; lower half buff washed with violet; chelae black, except for buff bases of both fingers.

These large crabs look amazingly like lava stones. When disturbed they grip stones tenaciously with their ambulatories and box with their open chelae. They can maintain position remarkably well against constant tugging and, when possible seize the human intruder's fingers and hang on like bulldogs, shedding their chelipeds less readily than any other crab with which I am acquainted. They will not come out of their niches to attack and do not even run away except when greatly disturbed on open ground. When annoyed they stridulate with the ridges of the manus rubbed squeakily against the underside of the carapace, chiefly beneath the third lateral lobe; the tubercles of this region described by Rathbun, however, are not well developed in our examples. The sound produced is like the high cry of a distant bird and is heard only when a crab is almost caught. It appears likely that these methods of defense are quite effective against natural enemies such as shore-birds and crab-eating raccoons.

Range: Nicaragua to Peru.

***Menippe obtusa*** Stimpson, 1859, p. 53 (7); Rathbun, 1930, p. 478, Sivertsen, 1934, p. 16. 5 specimens from Nicaragua (Cardon I. at Corinto). All in permanent tidepools (Zone 4). First record north of Costa Rica. All specimens taken were large females (35-43 mm.); many more, both sexes, seen but not captured.

Color in daylight, in air, brown to apricot orange. At night, under water, carapace and upper surface of chelipeds very dark green, almost greenish-black. Outer chelipeds, underside of carapace and ambulatories dull violet, the chelipeds speckled with blackish. Chelae brownish-black, teeth and tips white. Sternum and abdomen creamy blotched irregularly with violet; hair on distal segments of ambulatories dull green; posterior half of carapace sometimes also tinged with violet. Eyes red. Inner side of merus and carpal joints of chelipeds strawberry red.

Although doubtless common locally, these crabs are individually hermits, and are very retiring both night and day. Neither stridulation nor threat posture was observed. Unlike *M. frontalis*, *obtusa* spends its entire



life under water in the crevices between immovable rocks in tidepools. At night one large female went after a chiton in a fish trap she could not enter. When baited with a free chiton, she pulled it out of sight twice—once in daylight, once at night. This particular crab was finally caught by attracting her to the middle of a pool with a third chiton, at night, and by then jumping in and seizing her just as she was starting to pull away.

Range: Pacific coast of Nicaragua to Panama.

*Pilumnus gonzalensis* Rathbun, 1893, p. 240; 1930, p. 505. 3 specimens from Mexico (Tenacatita). First record south of Gulf of California. Among tidepool rocks (Zone 4). Grayish-brown.

*Pilumnus pygmaeus* Boone, 1927, p. 221; Rathbun, 1930, p. 515; Garth, 1946, p. 472. 3 specimens from Costa Rica (Port Parker, Culebra). Eggs in January. From weed in tidepools and on undersides of overgrown rocks, close to low tide (Zones 3, 4). Previously known only from the Galápagos.

*Pilumnus xantusii* Stimpson, 1860, p. 213; Rathbun, 1930, p. 486; Garth, 1946, p. 471. 2 specimens from Mexico (Sihuatenejo) and Costa Rica (Culebra). In *Pocillopora* coral (Zone 5). Dr. J. S. Garth kindly identified the Culebra specimen for me. The specimen from the Galápagos figured by Boone, 1927, p. 237, fig. 87B, as *Eriphides hispida* yg. should be referred to this species. Previously recorded only from Cape San Lucas and the Galápagos.

*Heteractaea lunata* (Milne Edwards & Lucas, 1843, p. 20); Rathbun, 1930, p. 532. Finnegan 1931, p. 644; Crane, 1937, p. 72. Not Boone, 1930, photo A, p. 127. 35 specimens from Mexico (Acapulco, Guatulco), Costa Rica (Port Parker, Culebra, Jasper), Colombia (Gorgona). Eggs in Jan. (Mexico), Jan., Feb. (Costa Rica), Mar. (Colombia). Our specimens were only found in *Pocillopora* coral (Zone 5); Rathbun reports specimens also from low tide rocks (Zone 3).

Range: San Diego, California (Faxon) to Chile.

*Ozius verreauxii* Saussure, 1853, p. 359; Boone, 1927, p. 223; 1929, p. 573; Rathbun, 1930, p. 540; Sivertsen, 1934, p. 17; Garth, 1946, p. 476. 35 specimens from Mexico (Puerto Angeles, Guatulco, Tangola-Tangola), Nicaragua (Cardon I. at Corinto, San Juan del Sur), Costa Rica (Port Parker, Golfito) and Colombia (Gorgona). 1 ovigerous female taken at Golfito in March. Under stones near low tide and in tidepools (Zones 3, 4).

Color pale olive buff to slate gray or chocolate brown except chelae, which are dark brown to black, three distal segments of ambulatories which are olive brown, and sternum and abdomen which are buff to

buffy-orange. A Guatulco specimen has the anterior third of carapace tinged with violet. Boone records bandings of coral at meral and carpal joints of ambulatories in the Galápagos; these were found on few Central American specimens, where they were represented by bright orange at joints of all legs and the entire length of the antennae. Young, plain light brown; very young almost white.

Range: Lower California to Ecuador; Galápagos.

*Ozius perlatus* Stimpson, 1860, p. 211 (83); Boone, 1927, p. 228; Rathbun, 1930, p. 543; Sivertsen, 1934, p. 17; Schmitt, 1939, p. 25; Garth, 1946, p. 477. 11 specimens from Mexico (Tangola-Tangola), Nicaragua (Cardon I. at Corinto, San Juan del Sur), and Costa Rica (Jasper I.). Under stones near low tide (Zone 3).

Carapace and chelipeds rose red; chelae ranging from very pale to dark brown. Posterior part of carapace sometimes apricot buff. Sternum buff. Abdomen apricot buff to rose red. Ambulatories rose red above, paler pinkish below. Dactyls straw colored. Ventral side of carapace in narrow rim just under antero-lateral margin, rose red like carapace. Cf. coloring in Galápagos (Garth, 1946).

These crabs, conspicuously colored to human eyes, are more active when their stones are overturned than are other sub-rock xanthids of the region. Often a number occur together under single stones.

Range: Cape San Lucas, Lower California, to Ecuador; Galápagos.

*Ozius tenuidactylus* (Lockington, 1877, p. 98); Glassell, 1935, p. 104; Garth, 1946, p. 479 and synonymy. *O. agassizii*, Rathbun, 1930, p. 544. 38 specimens from Mexico (Guatulco, Tangola-Tangola, Tenacatita), Nicaragua (Cardon I. at Corinto), Costa Rica (Port Parker, Piedra Blanca, Culebra, Cedro I., Ballenas, Golfito), Panama (Honda) and Colombia (Gorgona). Eggs in Feb. and Mar. (C.R. and Col.). Under stones near low-tide mark in tidepools (Zones 3, 4).

Reddish-brown or purplish to deep maroon, slightly paler beneath. Eyes bright red. Manus and dactyls of ambulatories covered with olive pile; chelae dark brown with white tips and teeth on major dactyl. Very young crabs (just under 5 mm.) pale brick red all over, lighter beneath; chelae lighter brown than in adult. Eggs purple to purplish-black.

Range: Gulf of California to Ecuador; Galápagos.

*Eriphia squamata* Stimpson, 1859, p. 56 (10); Boone, 1927, p. 231, 1929, p. 575, 1930, p. 143; Rathbun, 1930, p. 550; Hult, 1938, p. 13; Garth, 1946, p. 483. 35 specimens from Nicaragua (near Potosi R., Cardon I. at Corinto), Costa Rica (Port Parker,



Piedra Blanca, Ballenas, Uvita, Golfito), Panama (Honda) and Colombia (Gorgona). Under stones from mean low to high-tide marks, and, more rarely, in tidepools (Zones 2, 4). Once under mangrove root by mud flat (Zone 6). Eggs in Jan. and Feb. (Nic., C.R.), April (Col.).

General color dark but variable, ranging from slate gray through dark grayish-green to brown or black; often brownish or blackish mottled with greenish, or dark blue, blending admirably with algae in tidepool. Chelipeds like carapace, but fingers and ocular spines bright, ranging from burnt sienna to scarlet orange (Ridgway)—the latter shade the exact color of a red sponge that also grows in tidepool crannies, usually in small, longitudinal patches. Ambulatories banded with white or cream and purple, dark blue or brown. Underparts, and lower proximal part of manus and carpus cream. Often two narrow violet stripes extend down two-thirds of abdomen. Eyes olive green with brown centers. Eggs dark wine colored. Young (under 6 mm.) like adults, but lighter.

This crab is decidedly amphibious. I have seen it feeding both underwater on a mollusk in a tidepool, and at night, out of water, on tube worms. In day time I have only once seen it in the open out of water (though it frequently lies concealed under stones at low tide). This individual was scrambling on top of an exposed rock, but it had apparently been startled by a *Grapsus* out of its moist cranny or pool. All others were either well hidden or submerged. Saw one feeding in a submerged cranny holding what looked like a piece of mollusk in both claws and nibbling off it. Contents of 12 stomachs: Chiefly animal matter with some algae: (1) tiny, banded thread-algae, amphipods, 10 mm. hairy pink annelid with remains of hard tube, in only two pieces; (2) 1 megalops; (3) at least 3 megalopa and a few sand grains; (4) sand containing scum-like algae and a minute worm; (5) common red and black tidepool hermit crab (no shell); (6) tiny snails, mussels, worms, amphipods; (7) bits of algae and unrecognizable animal matter; (8-12) stomachs with thread or *Sargassum*-like algae in bits; 6 other stomachs were empty.

The first action of these crabs when attacked is to retreat. Their sight is relatively good: a moderate-sized male saw my fingers coming through the water 6 inches away, and backed repeatedly out of reach, reappearing each time in the opening of its cranny within one minute. Both males and females occasionally threaten with outspread chelipeds, but only when actively disturbed and retreat is impossible. The species is exceedingly common in tidepools and mid-tide stony zones, and ranks next to *Pachy-*

*grapsus transversus* and *Xanthodius sternberghii* in general abundance. The young do not threaten, but simply run away. The adults, too, are surprisingly fast out of water, when their stones are overturned, and are next to *Pachygrapsus* and *Grapsus* in speed, although none can compare with *Ocypode*.

Range: Gulf of California to Peru; Galápagos.

*Eriphides hispida* (Stimpson, 1860, p. 218 (90)); Boone, 1927, p. 236, not fig. 87B, p. 145; Rathbun, 1930, p. 552; Sivertsen, 1934, p. 18; Schmitt, 1939, p. 25; Garth, 1946, p. 487. 8 specimens from Nicaragua (Cardon I. at Corinto), Costa Rica (Port Parker, Jasper I.), Panama (Pearl Islands). Surf rocks, low down (Zone 1). Eggs in Feb. (C.R.).

Color purplish-brown above, rufous orange beneath; chelae bright rufous orange; hairs black; eggs bright scarlet. Young, around 20 mm. long, like adults in color.

On the outer surf rocks this species takes the place of its cousin, *Eriphia squamata*. The burr-like bodies of the crabs stick tightly in rock depressions and crevices close to low-tide mark when the tide is out, but when the water covers them they swim freely in the outermost pools. They have tremendous clinging strength, most of the gripping being done with the middle two pairs of ambulatories, and they do not shed the chelipeds easily. They are rather solitary, although where one is found another usually occurs within a few feet. They appear to stay near low-water levels even when the tide is high; that is, unlike *Grapsus*, they do not progress with the rising water. Although most of the feeding is almost certainly done underwater, I have seen several feeding in the air on serpulid worms in tubes. Dr. Beebe (1924, p. 131) suggests that the Galápagos representatives of the species may dispossess the sea-urchin makers of hollows in the lava. Unmistakable remains of a sea-urchin's mouthparts were found in the stomach of a large female from Corinto, along with sand and several algae fragments. Four other stomachs held no recognizable material except sand. These crabs often let themselves be literally torn to pieces rather than loose their foothold. Our mainland experience corresponds to that of Dr. Garth, who speaks of the vise-like grip of their powerful nippers in the Galápagos.

Range: West coast of Nicaragua to Panama; Galápagos. This is the first record north of Costa Rica.

*Domecia hispida* Eydoux and Souleyet, 1842, p. 235; Rathbun, 1930, p. 554; Finnegan, 1931, p. 647; Crane, 1937, p. 73; Garth, 1946, p. 489. 107 specimens from Mexico (Clarion I., Guatulco, Sihuatenejo, Acapul-



co), Costa Rica (Jasper, Uvita), Panama (Honda), Colombia (Gorgona). Always, on this coast, taken in *Pocillopora* coral (Zone 5). Eggs in Nov., Dec., May (Mexico), Mar. (Colombia). Carapace mottled brown and white, spines blackish. (Cf. Verrill's account of Atlantic specimens: "Light yellowish red, front darker; spines blackish. Among sponges and branches of corals, and in holes of dead corals and stones").

Range: South Carolina Brazil, eastern Atlantic, Indian and Pacific Oceans to American Coast; Gulf of California to Colombia; Galápagos.

*Trapezia cymodoce ferruginea* Latreille, 1825, p. 695; Boone, 1928, p. 240; Rathbun, 1930, p. 557; Finnegan, 1931, p. 645; Crane, 1937, p. 73; Hult, 1938, p. 13; Garth, 1946, p. 491. 778 specimens preserved from Mexico (Clarion I., Acapulco, Guatulco, Sihuatenajo), Costa Rica (Culebra, Port Parker, Jasper I., Uvita), Panama (Honda). A majority of the females were ovigerous in every lot examined; from the data now at hand, therefore (incl. Crane, 1937), this species is breeding in the northern part of its eastern Pacific range, that is, in Mexico and Clarion I., at least from November to May, and in the southern part, between Costa Rica and Gorgona Island, at least from January through March. On this coast the species was never taken except in living *Pocillopora* coral (Zone 5) where it is the most typical and abundant single species, not only of crabs but of all macroscopic invertebrates. Even the smallest heads, measuring less than a foot in diameter, have at least one pair—usually an adult male and ovigerous female—clinging far inside.

Color scarlet to scarlet orange, as described by Rathbun and Crane. Chelae are never black, dark brown at most, paler in young. Very young crabs (around 5 mm. in length) are pale pumpkin orange, instead of scarlet or scarlet orange. Large males are decidedly the brightest of all.

This species seems almost without question to be the pattern for a case of crab-shrimp mimicry. The shrimp (*Crangon ventrosus*) is always less numerous, although as typical of the *Pocillopora* habitat as is *Trapezia*. Its scarlet and black color matches the crab's structures. The shrimp always has the carapace sideways in the coral, with the cheliped folded out of sight; the crab sits frontways, the dark-tipped chelae folded in front of it. The true eye of the shrimp and one of the paired black spots over the first abdominal segment represent the crab's eyes. The black median stripe of the carapace resembles the dark chelae of the crab folded in front of it. Except for the shrimp, and *Carpilodes cinctimanus*, *Trapezia* alone of the coral crustaceans is brilliantly, not protectively, colored. All the others either

mimic the dead coral at the base of the head, are inconspicuously translucent, or match the live corals' browns and ochres. Furthermore, the shrimps and *Trapezia* are the only ones in the living part which do not loosen their hold when bothered. Since the majority of the coral heads live in water so shallow that the red rays have not yet been much weakened, it is possible that *Trapezia* is warningly colored.

Experiments should be performed, feeding *Trapezia* and protectively colored crabs from the same environment, to such presumably natural enemies as scorpaeonids and hermit crabs. Whether the red is actually a warning color, or whether it has developed unchecked merely because of *Trapezia*'s adoption of a well-protected niche, the crab is certainly amazingly successful; it may be that its numbers are kept down only by destruction in the larval stages.

Range: From Clarion Island and Gulf of California to Colombia and the Galapagos; Red Sea to Indo-Pacific area.

*Trapezia digitalis* Latreille, 1825, p. 696; Rathbun, 1930, p. 559; Crane, 1937, p. 73; Garth, 1946, p. 493. 110 specimens from Mexico (Clarion I., Sihuatenajo), Costa Rica (Uvita), Panama (Honda). The remarks about breeding seasons in *Trapezia cymodoce ferruginea* apply equally to this species. Like it, too, it occurs only in *Pocillopora*, at least in the eastern Pacific (Zone 5).

Color on this coast always rich chocolate brown to chestnut brown above, except for the palms and dactyls of the ambulatories, which are usually bright chestnut red (cf. Rathbun's quotation of bright color descriptions). In the very young, the anterior part of the carapace darkens first.

Range: Southern part of Gulf of California to Panama; Red Sea to Indo-Pacific region.

#### FAMILY GRAPSIDAE.

*Grapsus grapsus* (Linn., 1758, p. 630); Rathbun, 1918, p. 227; Boone, 1929, p. 577, 1930, p. 203; Sivertsen, 1934, p. 18; Crane, 1937, p. 77; Garth, 1946, p. 504. 5 specimens preserved from Mexico (Banderas Bay), Nicaragua (San Juan del Sur) and Colombia (Gorgona I.). The species was recognized or collected and examined, but not saved, at the following localities: Mexico (San Benito I., Cape San Lucas, Chamela Bay, Tenacatita Bay, Manzanillo, Sihuatenajo, Tangola-Tangola, Acapulco, Dulce River, Port Angeles); El Salvador (La Libertad, Gulf of Fonseca), Nicaragua (Corinto), Costa Rica (Port Parker, Murcielago Bay, Potrero Grande, Culebra, Braxilito, Piedra Blanca, Uvita, Golfito, Parida I.); Panama (Coiba I., Bahia Honda, Balboa). Ovigerous females were common in all localities during the observation period (No-



vember to April). The species is usually found only on large rocks exposed to surf and spray (Zone 1), occurring very rarely in protected harbors. At night it sleeps out of range of the tide, but during the day, keeps always just above it.

Along the tropical coast of the eastern Pacific, this crab is midway in coloration between the dark phase of the Atlantic, and the stage found in the Galápagos where apparently all the adults, male and female, are bright scarlet. In the present range, where large colonies were observed all along the coast, only rare, fully adult males are reddish, and these are usually chestnut. Throughout the winter and spring, red males (always more than 60 mm. long) numbered not more than 1 in 50 to 100. The exact proportion of adult males to adult females was not obtained, but at a conservative estimate there were 10 grown females to one male noticeably red in color. Males which do show red never have the overall scarlet developed in the Galápagos. A 72 mm. specimen from San Benito I. had the carapace chestnut brown, and sternum striations paler; legs and chelipeds were bright scarlet, and the underside bluish-white. One from Chamela Bay was similar, except that there were also white spots on the chestnut carapace. In other localities, smaller males had a chestnut tinge on the edges of the sternum and posterior part of the carapace, or had the carapace completely dark but the chelae, legs and sternum brilliant red.

Only at Tangola-Tangola did the color adumbrate that of the Galápagos colony. Although the crabs showed the usual local coloring in general, having the carapaces black spotted with blue, and the legs black spotted with bluish-green, the carapace in both sexes was frequently washed posteriorly with chestnut. Of six females, 34 to 60 mm. long and all ovigerous, three had a reddish tinge on the sternum only, while the chelae were deep wine-color. The smallest males showing any red were about 30 mm. long and had a chestnut tinge on the borders of the carapace and sternum, but not on the legs.

The agility of these crabs and their gregarious custom of sunning themselves in groups on damp rocks are well known. When forced into the water they are good swimmers, but return to the rocks as soon as possible. They are distinctly diurnal; at night they lie quietly in cracks or on open rocks above the reach of the tide, and are so torpid that they often can be picked up without making any effort to escape, whether or not a flashlight is used. They feed by plucking the fur-like algae from the rocks, using the spooned chelipeds alternately. However, although predominantly algae-eaters, there is no doubt but

that these crabs are also scavengers. Several times I have seen individuals eating dead fish and insects, and once a *Grapsus* seizing and eating a live dytiscid beetle. For an account of Galápagos specimens catching ticks on iguanas and eating martins, see Beebe, 1924, pp. 93 and 121, or Boone, 1927, p. 246 ff.

Forty stomachs were examined with the following results: Practically all contained fine rock algae, usually more or less mixed with sand, such as is found washed up around the bases of the algae.

Ten stomachs contained one or more of the following: bryozoans, tiny mussels, barnacles, hydroids.

The chief enemies in many localities are doubtless nocturnal crab-eating raccoons; twice raccoon tracks were found beside *Grapsus* remains. Once a grackle was seen to seize a crab, having stalked it from around a projecting rock. Surf fishes must often catch unwary crabs that are washed into the sea.

Range: Tropical and subtropical shores of America and of the eastern Atlantic. The subspecies *G. grapsus tenuicrustatus* inhabits the Indo-Pacific region.

*Geograpsus lividus* (Milne Edwards, 1837, p. 85); Rathbun, 1918, p. 232; Boone, 1927, p. 253; Sivertsen, 1934, p. 19; Schmitt, 1939, p. 25; Garth, 1946, p. 506. 19 specimens preserved from Mexico (Tenacatita, Guatulco), Nicaragua (San Juan del Sur), Costa Rica (Port Parker, Culebra, Jasper I.), Colombia (Gorgona I.). Many others seen but not saved. Eggs seen from Nov. to April (Mexico to Colombia). Under large loose stones on rock shores, or with substratum of coral and sand; rarely in similar localities near mangroves; lives well above low tide marks (Zone 2).

Ground color of carapace varying from bright yellowish-green through pale emerald to black; reticulations or marblings contrasting, black or purple on light crabs, green on black ones. Chelipeds sometimes tinged with orange, or rusty orange above mottled with black; legs blue green to purplish; hairs yellow. Eggs purple. Young (7 mm. long), very pale green with black reticulations very narrow; chelipeds buff. Have not seen on the west coast the coloration recorded by Rathbun ("Yellowish red with reticulating lines or patches of a darker red or purplish; sometimes wholly red."). This may be typical of the east coast member of the species.

Of five stomachs containing food, one held remains of a minute sea urchin, two, insect remains (probably beetles), two amphipods, and two, a few bits of gravel.

Range: Florida keys to Brazil; Bermudas; Lower California to Chile; Galápagos; Hawaiian Islands.



*Goniopsis pulchra* (Lockington, 1877, p. 152); Rathbun, 1918, p. 239. 43 specimens preserved from Mexico (Chamela), Nicaragua (Corinto), Costa Rica (Culebra, Puntarenas, Golfo), Panama (Honda), Colombia (Gorgona I.) and Ecuador (Puerto Bolivar). Eggs in Dec. (Nic.), Feb. (C.R.). Among mangroves, especially along banks of estuaries and lagoons, close to water line (Zone 6). Rarely in almost fresh water, with no mangroves within several hundred yards.

General color dark above with light spots; chelipeds and legs reddish; females duller. In more detail the coloration is as follows: ground color of carapace usually jet black; the round to elongate spots and bars are pale olive brown to pale buff, fading to white on sides and posterior margins of carapace. These markings are very variable in size and number, but a few large ones are almost always present on postero-lateral sides of carapace. Chelipeds bright rufous to brilliant scarlet in males, except for black tubercles and creamy dactyls and distal part of manus; in females and young the merus and carpus are usually blackish-red to blackish-brown with other segments yellowish-cream washed with orange. Merus of ambulatories in males sometimes bright scarlet, sometimes only tinged with rose posteriorly; other segments pale olive brown to pumpkin orange, or light reddish, the manus spotted with black and white; all segments with black hairs and white spot at base of each hair. Underparts creamy except external maxillipeds which are pure white; legs of female without red, plain buff marked with black. Eggs dull purple. The red develops late; young crab (about 10 mm.) black with small cream spots all over except for manus and chelae which have black dorsal ridge, apricot buff central portion, and cream pollex and lower half of manus. A 12 mm. specimen was olive green all over except for typical white spots on postero-lateral sides of carapace; underparts, manus, dactyls and chelae all cream. A single male at Gorgona was much redder than any others seen, the color continuing even on the carapace, rather as in the *Atlantic cruentata*.

The steep banks of estuaries and mangrove swamps proper are often honeycombed with the burrows of this crab. Each burrow typically has two or more entrances, often close together; they tend to run parallel, close to the surface, for long distances, although holes more than three or four feet deep usually go down to water level, then back up and in; often they lead into each other or have common entrances. At Balleas the holes were everywhere on a low muddy flat that was always completely covered at high water; very few mangroves grew here; the ground was honeycombed,

with many tunnels parallel to the surface, although a few deep holes existed; some individuals lived under old mangrove logs.

When pursued, these crabs use any hole at all to escape; unlike *Uca* they apparently have little sense of property.

Range: From Magdalena Bay, Lower California, to Peru.

*Pachygrapsus transversus* (Gibbes, 1850, p. 181); Rathbun, 1918, p. 244; Boone, 1927, p. 255, 1929, p. 577; Pesta, 1931, p. 179; Finnegan, 1931, p. 649; Sivertsen, 1934, p. 19; Schmitt, 1939, p. 25; Garth, 1946, p. 507. 121 preserved from Mexico (Sihuatenango, Tangola-Tangola), El Salvador (G. of Fonseca), Nicaragua (Cardon I. at Corinto, near Potosi R. in Gulf of Fonseca, San Juan del Sur), Costa Rica (Port Parker, Culebra, Uvita), Panama (Honda), Colombia (Gorgona I.). Eggs are plentiful everywhere from Nov. to March. This species is the most abundant and ubiquitous of shore crabs; it is found in all zones where there are stones or rocks, from moderately brackish water to open coasts, on muddy, sandy or stony substrata, in tidepools, and even among mangrove roots or logs with stones among them (Zones 1, 2, 3, 4, 6, 7, 8). It fails to occur only in coral, open mud or open sand, although it is rare on the most exposed surf-beaten rocks where *Grapsus* and *Eriphides* are typically found. The largest crabs are always found on the larger rocks, small ones stay near pools or under small stones. Length of largest male 13.5 mm.; largest ovigerous female 11.5; smallest ovigerous female 6.5 mm.

There is considerable color variation, the greenest crabs being among green weed, and the darker ones on dark stones. Typically, the crab is very dark green or black with bright green marblings or striations; longitudinal bar of bright green on intestinal region, and a transverse line of this color in both proximal and distal joints of carpus; chelae and lower three-quarters of manus creamy; upper and lower sides of ambulatories same as carapace and faintly banded with cream.

The following notes made at Cardon I., Corinto, concern behavior which is typical of these crabs everywhere along their Pacific coast range. "Dec. 31. Low tide. 13 small *Pachygrapsus* seen in an area near low-tide level measuring 1 × 3 feet, composed of large and small stones exposed in a pool between boulders. All of the crabs, in both sun and shade, were out of water feeding on algae as fast as they could, using their chelae alternately in perfect rhythm. Their bodies appeared very green and algae-like in the sun, yet in the shade the darker black markings gave the tone, so that, like the algae in shadow, they appeared almost black. Twenty-five minutes after low tide



the water had risen a good three inches in the pool, although it was still quiet. Nevertheless, most of the best algae was now under water, and not one of the 13 crabs was in sight. Evidently, they prefer to feed in the air, and since the richest algae beds are uncovered in these near-low-tide zones for such a very short time, the reason for their haste in feeding is evident. During the entire morning I saw only one *Pachygrapsus* feeding under water, and that was in a half-hearted fashion for a few moments only.

"The original 13 had no territorial precincts, individuals sometimes feeding alone on a rock, sometimes within three inches of a neighbor, and moving on to a new spot two or three inches away after a minute or so. Could see a movement of mine a good foot or more away, and would stop eating at once and run into a crevice. A half-grown *Grapsus* startled a *Pachygrapsus* away from its algae; it ran four inches and started feeding again under a ledge, while the *Grapsus* took up grazing in the *Pachygrapsus*' first site. Another *Pachygrapsus* backed into a grazing snail, the snail struck out viciously with its foot, and the *Pachygrapsus* ran away in this case too, although it was fully as large as the snail.

"The larger *Pachygrapsus* dare to get farther from the pools, grazing on top of the large boulders in damp hollows. They are startled by a human movement as much as two feet away.

"These crabs are active and feed at night, but not as much as during the day. They appear brown at night, like the weed and rocks, in the light of an electric torch."

Among their enemies are carnivorous tidepool fish; we took them from the stomach of a blenny, *Malacosteus xonifer*, and of the common tidepool goby, *Bathygobius soporator*.

Range: Cosmopolitan in the tropics.

*Sesarma sulcatum* Smith, 1870, p. 156; Rathbun, 1918, p. 289. 10 specimens from Costa Rica (Negritos, Ballenas, Golfito). In gravelly mud along a lagoon shore, on banks of drying streams (nearly or completely freshwater), and in slightly brackish mangrove mud (Zones 6, 7).

Large male from Golfito: Carapace and legs plain dark brownish-gray; cheliped merus, carpus, upper half of manus and upper basal part of movable finger chocolate brown; lower half of manus and rest of chelae bright creamy yellow; sternum, abdomen and all except manus and dactyls of undersides of ambulatories light buff; undersides of manus and dactyls grayish-brown. Ovigerous female: with yellow line across front, rest yellow brown all over mottled with black except chelipeds which are as follows: merus and carpus cream with striations and tubercles maroon. Manus

and chelae entirely cream except maroon striations on upper margin. Underparts a cream washed with gray. Eggs chocolate brown.

One specimen found in stomach of white ibis, Corinto.

The females and young, neither in our series nor in that at the United States National Museum, have the full number of spinules on the dactyl. Typical counts of our specimens are as follows: female, 4.8 mm., no side tooth, no dactyl spinules, legs slightly more slender than in adult (this specimen was taken at Ballenas in midst of a colony of this species, so there is no reasonable doubt of the identification); male, 5.1 mm., has side tooth, beginning of spinules, thicker legs; ovigerous female, 14 mm., 9 dactyl spinules; male, 17 mm., 9 dactyl spinules; male, 20 mm., 10 dactyl spinules. A conspicuous short longitudinal ridge, not mentioned in the descriptions, runs along middle of outer surface of palm in male; this ridge is present also in U.S.N.M. specimens.

Range: From La Paz, Lower California to Panama.

*Sesarma rhizophorae* Rathbun, 1906, p. 99; 1918, p. 294. 2 specimens, male 8.3 mm., ovigerous female, 8.4 mm., from Costa Rica (Puntarenas and Ballenas). Among mangrove groves (Zone 6). Compared with holotype and other specimens in U. S. National Museum. Agrees perfectly except that the granules are more strongly developed in the holotype than in our specimen.

Range: Known only from Costa Rica.

*Aratus pisonii* (Milne Edwards; 1837, p. 185); Rathbun, 1918, p. 323. Boone, 1931, p. 207; Finnegan, 1931, p. 651. 16 specimens preserved from Nicaragua (Corinto, San Juan del Sur), Costa Rica (Port Parker, Ballenas, Golfito), Panama (Honda). On west coast of America, always on mangrove boughs, well above water (Zone 6).

Typical coloring: entire gastric portion of carapace nopal red (Ridgway); surrounding parts, including front and antero-lateral margins, off-white marbled with dark brown. Chelipeds nopal red. Inner parts and tips of dactyls flame scarlet. Hairs black with straw tips. Eyes olive gray. Eye stalks nopal red with black dots. Ambulatories dark gray marbled with black and, on merus, washed with orange-brown. Sternum and abdomen white. Underside of ambulatories peach gray.

Range: Coasts of America, from Florida to Brazil and from Nicaragua to Peru.

#### HABITAT ZONES.

The habitats of the intertidal brachyuran crabs (as limited on p. 69) taken by the Eastern Pacific Expedition proved to divide themselves into nine quite distinct zones. These may be listed as follows:



1. *Surf Rocks*.
2. *Stones near Mid-tide Levels*: that is, tidal stones well above low tide levels.
3. *Stones near Low-tide Levels*: tidal stones only briefly uncovered by the tide.
4. *Tidepools*.
5. *Coral: Pocillopora*.
6. *Mangroves*: swamps and estuary banks.
7. *Mudflats*: open, unshaded.
8. *Sheltered Beaches*: sandy-mud or sandy.
9. *Exposed Beaches*: sandy.

It will be noted that in Zones 1-5, the substratum is hard, while in 6-9 it is more or less soft. In 1-5 and in 9, the salt concentration of the water is high, approaching that of open ocean; in 6, 7 and 8 it is low, ranging from almost fresh to around 75% of oceanic salinity. Unfortunately, no exact salinity analyses were made of these various habitats, except in the case of a few species of *Uca*. Obviously, the nine zones could be divided into a number of smaller niches, but this subdivision must await future, more exact investigation in the field.

These nine habitats will be described below in more detail, and a list of the crabs occurring in each will be given. It must be emphasized that these are only the records made by the present author. Some of the observations, such as the occurrence of *Grapsus* in the surf zone, have been repeatedly recorded by previous writers: others, such as the restriction of certain species to *Pocillopora* coral, although well known to even amateur field naturalists, appear never to have been published in the reports of this area. Although years of field work would be needed to make a complete report on this subject, still the usual habitats of the more common species are without question those given. The ecologic ranges of the rarer forms will, however, unquestionably be extended to other habitats. The following species included in the present report were also taken on the *Zaca* in deeper water: *Teleophrys cristulipes*, *Mithrax pygmaeus*, *M. areolatus*, *Anaptychus cornutus* and *Xanthodius stimpsoni*. A few other species, such as *Daldorfia garthi*, which were taken only on shore or in *Pocillopora* on the *Zaca*, have been reported by the Hancock and other expeditions from deeper water as well.

In spite of the above limitations, one of the clearest results of the present study is the restriction of the vast majority of species to only two or three niches having a number of characters in common—for example, tidepools, stones near the low-tide level, and *Pocillopora* coral, or mangroves and open mudflats. Finally, a considerable number appear to be confined to a single zone.

The following lists represent the summarized results of daily collections and notes made on 79 different species from more than 50 geographic localities. More than 3,500 specimens were collected and, of the more common forms easily identified at sight—for example, *Grapsus*, *Goniopsis* and *Ocypode*—literally thousands of additional individuals were seen and their habitats noted, although no specimens were collected.

The zone references in parentheses following species names refer to the other zones in which that form was taken, and are given for purposes of easy cross-reference.

In the concluding section is given a summary of the relative richness of habitat zones.

**Zone 1. Surf Rocks.** This habitat consists of exposed rocks and cliffs to which algae are usually attached. Technically, it should be divided into two parts, an upper region dampened only by spray or exceptional tides, and a lower zone which is covered twice daily by normal tides. Since the scanty brachyuran fauna is little affected by these distinctions, they are not observed in this list. The four species found in the zone are the following:—

**Majidae:**

*Acanthonyx petiverii*. Also in tidepools (4).

**Xanthidae:**

*Eriphides hispida*.

**Grapsidae:**

*Grapsus grapsus*.

*Pachygrapsus transversus*. Rare here; also present in all other zones except coral (5) and exposed beaches (9).

**Zone 2. Stones Near Mid-tide Levels.** This zone is represented by tidal stones between mean and high-tide marks. It is distinguished from the next chiefly by the scarcity or absence of algae, serpulids, corals and other growths upon the under sides of the stones. This habitat occurs frequently between the ends of protected beaches and the boulders or cliffs which form the adjacent promontory.

**Xanthidae:**

*Leptodius taboganus*.

*Xanthodius sternberghii*. Also under stones near low tide (3) and in tidepools (4).

*Eurypanopeus planus*.

*Menippe frontalis*.

*Eriphia squamata*. Also in tidepools (4) and, rarely, among mangroves (6).

**Grapsidae:**

*Geograpsus lividus*.

*Pachygrapsus transversus*. Also present in all other zones except in coral (5) and on exposed beaches (9).

**Ocypodidae:**

*Uca panamensis*.



**Zone 3. Stones Near Low-tide Levels.** This zone is represented by tidal stones near low-tide marks. They are uncovered at most only an hour or so during each tidal period, and during neap tides may be underwater for days at a time. Therefore, since the undersides of the stones never dry out, they are encrusted with a varied sessile fauna and flora, consisting chiefly of algae, sponges, corals, bryozoans, serpulid worms and tunicates. Here gather also many non-sessile animals, such as starfish, serpent stars, holothurians, worms, mollusks and snapping shrimps. As is to be expected, the crab fauna is rich, particularly in spiders. Most of the species cling upside down to the growth on the stones.

#### Majidae:

*Eucinetops panamensis*. Rare here; typically present in tidepools (4).

*Pelia pacifica*. Also in tidepools (4) and coral (5).

*Herbstia tumida*. Also in coral (5).

*Thoe sulcata*. Rare here; typically present in tidepools (4) and coral (5).

*Pitho sexdentata*.

*Anaptychus cornutus*. Also in tidepools (4) and coral (5).

*Mithrax denticulatus*. Rare here; typically present in tidepools (4) and coral (5).

*Teleophrys cristulipes*. Rare here; typically present in tidepools (4) and coral (5).

#### Parthenopidae:

*Daldorfia garthi*. Usually found in deeper water.

#### Xanthidae:

*Daira americana*. Rare here; typically present in coral (5).

*Cyclothanops vittatus*. Also in coral (5).

*Leptodius taboganus*. Also under stones near mid-tide levels (2).

*Xanthodius sternberghii*. Also under stones near mid-tide levels (2) and in tidepools (4).

*Xanthodius stimpsoni*. Also in tidepools (4) and coral (5).

*Lophoxanthus lamellipes*. Also in tidepools (4) and coral (5).

#### Xanthidae:

*Pilumnus pygmaeus*. Also in tidepools (4).

*Ozius verreauxii*. Also in tidepools (4).

*Ozius perlatus*.

*Ozius agassizii*. Also in tidepools (4).

#### Grapsidae:

*Pachygrapsus transversus*. Also present in all other zones except in coral (5) and on exposed beaches (9).

**Zone 4. Tidepools.** This habitat is too well known to need discussion, except to point out that tidepools are usually in an exposed position, and that their rocky, uneven sides and bottoms give excellent support for many

kinds of algae. It is usually in the algae that most of the following crabs are found.

#### Majidae:

*Eucinetops panamensis*. Also under stones near low-tide levels (3).

*Acanthonyx petiverii*. Also on surf rock (1).

*Pelia pacifica*. Also under stones near low-tide levels (3) and in coral (5).

*Thoe sulcata*. Also under stones near low-tide levels (3) and in coral (5).

*Anaptychus cornutus*. Also under stones near low-tide levels (3) and in coral (5).

*Mithrax denticulatus*. Also under stones near low-tide levels (3) and in coral (5).

*Mithrax orcutti*.

*Teleophrys cristulipes*. Rare here; typically present in coral (5).

*Microphrys platysoma*. Also under stones near low-tide levels (3) and in coral (5).

#### Xanthidae:

*Actaea dovii*. Also in coral (5).

*Actaea sulcata*. Rare here; typically present in coral (5).

*Xanthodius sternberghii*. Also under stones near mid-tide (2) and low-tide (3) levels.

*Xanthodius stimpsoni*. Also under stones near low-tide levels (3) and in coral (5).

*Lophoxanthus lamellipes*. Also under stones near low-tide levels (3) and in coral (5).

*Metapocarcinus concavatus*.

*Menippe obtusa*.

*Pilumnus gonزالensis*.

*Pilumnus pygmaeus*. Also under stones near low-tide levels (3).

*Ozius agassizii*. Also under stones near low-tide levels (3).

*Ozius verreauxii*. Rare here; typically present under stones near low-tide levels (3).

*Eriphia squamata*. Also under stones near low-tide levels (2) and, rarely, among mangroves (6).

#### Grapsidae:

*Pachygrapsus transversus*. Also present in all other zones except in coral (5) and on exposed beaches (9).

**Zone 5. Coral (*Pocillopora*).** This distinctive habitat zone is included in the present paper on intertidal crabs for two reasons. First, although the coral usually lies at least three feet and usually from six to eighty or more feet under water, it is occasionally partially exposed during spring tides. Second, its fauna overlaps that of the tide zones, rather than that of the deeper littoral. Associated with the very characteristic bryozoan fauna, are equally well-marked animals of other groups, particularly the snapping shrimp, *Crangon ventrosus*, as well as numerous other shrimps, serpent stars, worms, and occasional mollusks and fish. More than fifty heads of coral, ranging in diameter from six inches to more than



feet, were carefully hammered open and their inhabitants collected. Of the 21 species of brachygnathous crabs found, nine were never taken by us in any other habitat.

#### Majidae:

*Pelidnota pacifica*. Also under stones near low-tide levels (3) and in tidepools (4).

*Herbstia tumida*. Also under stones near low-tide levels (3).

*Thoe sulcata*. Also under stones near low-tide levels (3) and in tidepools (4).

*Anaptychus cornutus*. Also under stones near low-tide levels (3) and in tidepools (4).

*Mithrax denticulatus*. Also in tidepools (4); rare under stones near low-tide levels (3).

*Mithrax pygmaeus*.

*Teleophrys cristulipes*. Also, rarely, under stones near low-tide levels (3) and in tidepools (4).

*Microphrys platysoma*. Also under stones near low-tide levels (3) and in tidepools (4).

#### Xanthidae:

*Carpilodes cinctimanus*.

*Actaea dovii*. Also in tidepools (4).

*Actaea sulcata*. Also, rarely, in tidepools (4).

*Daira americana*. Also, rarely, under stones near low-tide levels (3).

*Tedaeus spinulifer*.

*Cyclothanops vittatus*. Also under stones near low-tide levels (3).

*Anthodius stimpsoni*. Also under stones near low-tide levels (3) and in tidepools (4).

*Polphoxanthus lamellipes*. Also under stones near low-tide levels (3) and in tidepools (4).

*Micropanope xantusii*.

*Pilumnus xantusii*.

*Heteractaea lunata*.

*Domecia hispida*.

*Trapezia cymodoce ferruginea*.

*Trapezia digitalis*.

Zone 6. Mangroves. This zone includes both swamps, estuaries, and the edges of lagoons — wherever mangroves are found. Muddler crabs (*Uca*) are the most typical and abundant crabs of these brackish areas, the characteristics of which are too well known to require further comment. It should only be noted that small stones are often present near the edge of a swamp and that some species, particularly *Eurypanopeus transversus*, do not occur where stones are absent. Below are included only those species found among the mangrove roots or in their shade. Those living on nearby mudflats are in subsequent categories (7 and 8).

#### Xanthidae:

*Panopeus purpureus*. Also on mudflats (7).

*Eurypanopeus transversus*. Among stones only. Also among stones on mudflats (7) and sheltered stony-mud beaches (8).

*Eurytium tristani*. Also on mudflats (7).

#### Grapsidae:

*Eriphia squamata*. Rare here; present among stones near mid-tide levels (2) and in tidepools.

*Goniopsis pulchra*.

*Pachygrapsus transversus*. On roots and stones only. Also present in all other zones except in coral (5) and on exposed beaches (9).

*Sesarma rhizophorae*.

*Sesarma sulcatum*. Also on mudflats (7).

*Aratus pisonii*. Among mangrove branches only.

#### Ocypodidae:

*Uca zaca*.

*Uca schmitti*.

*Uca brevifrons*.

*Uca tomentosa*.

*Uca umbratila*.

*Uca inaequalis*. Also on mudflats (7).

*Uca tenuipedis*.

*Uca batuenta*.

*Uca crenulata*.

*Uca argillicola* (in clayey mud); (type series only).

*Uca limicola* (type series only).

*Uca latimanus*. Rare here; typically on sheltered beaches (8).

Zone 7. Open Mudflats. In this and the following zone (8), there is a complete lack of shade, but mangroves are almost always at least within sight of the human eye. The richest areas are close to the vegetation; the center of the flats are usually lacking in crabs. As in the preceding zone, some of the species below are found only or chiefly where some stones are present in the mud.

#### Xanthidae:

*Panopeus purpureus*. Also among mangroves (6).

*Panopeus chilensis*.

*Eurypanopeus transversus*. Among stones only. Also among mangroves (6) and on sheltered beaches (8).

*Eurytium tristani*. Also among mangroves (6).

#### Grapsidae:

*Pachygrapsus transversus*. Among stones only. Also present in all other zones except in coral (5) and on exposed beaches (9).

*Sesarma sulcatum*. In gravelly mud only. Also among mangroves (6).

#### Ocypodidae:

*Uca princeps*. Also on sheltered beaches (8).

*Uca heteropleura*. Also on sheltered beaches (8).

*Uca styliifera*. Also on sheltered beaches (8).

*Uca insignis*. Also on sheltered beaches (8).

*Uca macrodactyla*.

*Uca schmitti*.

*Uca galapagensis*.



*Uca oerstedii*.

*Uca inaequalis*. Also among mangroves (6).

*Uca saltitanta*.

*Uca beebei*. Also on sheltered beaches (8).

Zone 8. *Sheltered Beaches*. These include stretches of sandy-mud or sandy shores, unshaded, covered at high tide by brackish water. Open water, whether estuary or narrow-mouthed bay, is usually closer than in Zone 7.

Xanthidae:

*Eurypanopeus transversus*. Only among occasional stones. Also among mangroves (6) and on mudflats (7).

Grapsidae:

*Pachygrapsus transversus*. Only among occasional stones. Also present in all other zones except in coral (5) and on exposed beaches (9).

Ocypodidae:

*Ocypode gaudichaudii*.

*Ocypode occidentalis*. Rare here; typically on exposed beaches (9).

*Uca princeps*. Also on mudflats (7).

*Uca heteropleura*. Also on mudflats (7).

*Uca stylifera*. Also on mudflats (7).

*Uca insignis*. Also on mudflats (7).

*Uca festae*.

*Uca beebei*. Also on mudflats (7).

*Uca stenodactyla*.

*Uca deichmanni*.

*Uca latimanus*.

*Uca terpsichores*.

Zone 9. *Exposed Beaches*. This zone is always sandy, and the concentration of the water approaches that of normal open ocean.

Ocypodidae:

*Ocypode occidentalis*. Also on sheltered beaches (8).

#### CONCLUDING REMARKS ON FIELD OBSERVATIONS.

A paper such as this one, which is composed largely of field notes, can never be prepared without a feeling of deep dissatisfaction. The individual observations are so fragmentary, the basic problems involved so little understood, that the only excuse for putting the notes on record lies in the scarcity of field observations of any kind. With these facts in mind, it seems worthwhile to conclude with a few remarks on the ecology, coloration and behavior of these crabs, which may suggest lines for worthwhile future study. Planned research in any of these directions would add not merely to knowledge of the Brachyura, but also to the clarification of vital problems of theoretical biology. All such studies on these north-tropical Eastern Pacific shores are facilitated by the characteristic warm waters, relatively well-watered shores, high tides and adequate bays and gulfs, which unite

to encourage an especially rich and varied littoral brachyuran fauna.

Thanks to the tireless work of Mary J. Rathbun, and, more recently, of Susan Finnegan, Steve Glassell and John S. Garth, the taxonomy and geographical distribution of the shore crabs of the tropical eastern Pacific are becoming very well organized and understood. These questions will not be considered here, except to remark on the convenience, for field workers, of the relatively wide ranges of most of the common shore species, which often extend from Cape San Lucas to Panama and beyond, as well as the occurrence of a number of species which are cosmopolitan in the tropics.

1. RICHEST COLLECTING STATIONS: Our experience on the *Zaca* showed a number of localities where crab collecting was especially fruitful, and a number of others where shore life in general and the crab fauna in particular were so poor that the results were scarcely worth the effort of landing. For the benefit of future workers, these richer bays are listed here. It should be kept in mind, however, that local shifts in population, the laying of pipe lines, or natural or artificial swamp drainage may swiftly ruin the best of collecting grounds. On the other hand, the richest colonies are often found near sewer outlets and garbage dumps, provided the water is not polluted by oil or chemicals. Examples of such richness, which are due at least partly to nearby habitation, are the entrance to Corinto harbor and certain localities around the mouth of the Panama Canal.

During the Eastern Pacific *Zaca* Expedition of 1937-1938, and my later (1941 and 1944) trips to Panama and Ecuador, the most fruitful localities, from the point of view of inter-tidal crab populations, were the following (see map, p. 70):

#### Mexico:

Acapulco. Moderately good; chiefly rock short habitats and coral.

Tangola-Tangola. Of the three adjacent bays, Guatulco, Santa Cruz and Tangola, the latter was by far the best. Stony, rocky and sandy beach and tidepool habitats; *Pocillopora*; the extensive lagoons with mangroves, were not investigated for crabs.

#### Nicaragua:

Corinto. Excellent. Many habitats, from marine stones, rocks and tidepools at Cañon Island, to brackish water mudflats and mangroves.

#### Costa Rica:

Port Parker. Excellent. Many habitats accessible, from coral and marine rocks, stones and tidepools at Abajos Point to fresh-water streams. Limited mangrove and mud-flat areas.



Culebra. Mediocre stony shore populations, but good *Pocillopora* easily available; the latter were in individual heads rather than in reef form.

Piedra Blanca. Good rock, stone, beach and tidepool habitats.

Gulf of Nicoya. The upper portion, around Puntarenas, was excellent for brackish water, mangrove and mud-living species. Naturally, no coral was found here, but excellent *Pocillopora*, in extensive reef formation, occurred toward the mouth of the Gulf around Jasper Island. Ballenas Bay, beside the mouth, had a good lagoon fauna (mangrove and mudflat), but the stony shore and tidepool collecting was poor.

Uvita Bay. Moderately good exposed stony reef, rock and beach collecting; *Pocillopora* present; also a good fresh-water stream.

Golfito, in Gulf of Dulce. This practically uninhabited locality was wonderfully rich in all mud- and sandy-mud-living forms, having extensive protected mudflats and mangroves, and fresh-water rain-forest streams. We have heard, however, that it has been spoiled, zoologically speaking, by one of the fruit companies.

#### Panama and the Canal Zone:

Bahia Honda. Good, semi-exposed stony shore and beach collecting; also fair *Pocillopora*, mudflats and brackish streams.

Panama City and Balboa. The beach at Bellavista and the mangrove pocket known as La Boca still had adequate brackish-water crab populations as late as 1944. They had deteriorated, however, since 1941, because of wartime construction at La Boca and some apparently natural silting up of mudflats at Bellavista (cf. Crane, 1941).

#### Colombia:

Gorgona Island. (The only locality visited in Colombia). Moderately good shore-crab populations.

#### Ecuador:

Puerto Bolivar (at mouth of Guayas River). Excellent sheltered beach, mudflat and mangrove crab fauna here and on nearby Jambeli Island. The swamps were being drained in 1944, but the crab colonies, particularly of *Uca*, are so extensive that they should be safe for some years.

Guayaquil. The few, nearly fresh-water forms which can live here were all thriving in 1944. The apparently endemic *Uca festae* is abundant.

2. ABUNDANCE. The numbers of individuals of the various species in the expeditions' collection give no clue to their actual abundance in the field for three reasons: first, no effort was made to make collections from this point of view; second, some of the more common forms, such as *Eriphides* of the surf zone, were difficult to reach and collect

intact; third, extensive representations of some of the best known species, such as *Grapsus* and *Goniopsis*, were not considered necessary.

Field notes made on the Zaca from Acapulco to Panama, however, leave no doubt as to which were the most abundant species among these intertidal crabs. Naturally, it is impracticable to compare numbers of a large form such as *Grapsus* with a small one such as *Pachygrapsus*, or the dominant form in one habitat zone with that in another, but irrespective of zones, the following species are certainly among the most widely distributed and generally accessible, observable, abundant and successful of all the crabs within the area under discussion; they are arranged in taxonomic order:

*Xanthodius sternberghii* (Zones 2, 3, 4).

*Eurypanopeus planus* (Zone 2).

*Eriphia squamata* (Zones 2, 3, 4).

*Trapezia cymodoce ferruginea* (Zone 5).

*Grapsus grapsus* (Zone 1).

*Geograpsus lividus* (Zone 2).

*Pachygrapsus transversus* (Practically ubiquitous, except in coral and on open sandy beaches).

*Ocypode occidentalis* (Zone 9).

*Ocypode gaudichaudii* (Zone 8).

Of course, many other species, e.g. a number of *Uca*, are locally abundant.

A thorough study of any one of these readily available species would be certain to yield excellent results.

Spider crabs are notable for the absence of numerically abundant species.

3. HABITATS. Conditions naturally vary locally, but the following species are most universally present in their respective zones.

Zone 1. Surf Rocks. *Grapsus grapsus*.

Zone 2. Stones near mid-tide levels. *Xanthodius sternberghii*, *Eriphia squamata*, *Uca panamensis* and *Eurypanopeus planus* are practically always present in the mixed sand and stony area at ends of protected beaches.

Zone 3. Stones near low tide levels. No species outstanding, since local conditions vary greatly.

Zone 4. Tidepools. Same remarks as for Zone 3.

Zone 5. Coral (*Pocillopora*). *Trapezia cymodoce ferruginea*.

Zone 6. Mangroves. *Goniopsis pulchra*; *Aratus pisonii*.

Zone 7. Open mudflats. No species outstanding.

Zone 8. Sheltered beaches. *Ocypode gaudichaudii*.

Zone 9. Exposed beaches. *Ocypode occidentalis*.

In regard to the richness of habitat zones



in number of species in the collections, tide-pools and *Pocillopora* coral lead with 22 species each, followed by mangroves with 21, low-tide levels with 20, mudflats with 17 and protected beaches with 14. The poorest are exposed beaches with 1 species (*O. occidentalis*), surf rocks with 4 and stones at mid-tide levels with 8.

A field in which excellent detailed work could be done on this coast concerns the structural and physiological adaptations to niches. For example, the high proportion of hairy or decorated species which cling to the encrusted stones of low tide regions is always striking when contrasted with the predominantly naked or scarcely pilous forms of the mudflats. Subdivisions of this subject, concerning the variations in attachment, amount and kind of decoration in spider crabs are most interesting; a few examples have been given in the systematic part of this paper.

Again, the variations in foot structure, for clinging versus digging functions, for example, show beautiful adaptations. Finally, although work has been done on desiccation tolerance among east coast shore crabs (i.e. Pearse, 1936), west coast forms, which are subjected to exceptionally high and low tides, have not been investigated. Extreme adaptiveness to alternate and irregular submergence and aestivation must have been developed, furnishing challenging material for research. In *Uca* this tolerance is particularly striking.

4. COLOR. The wide prevalence of protective coloration was, as usual, the most striking crab color characteristic on the Pacific expeditions. During the exceptional opportunities presented by the *Zaca* trips, the adaptive variability in accordance with the terrain could be well appreciated. This was demonstrated both by different populations of the same species, and by individuals within populations. The variability was most notable in fairly active crabs on stony, sandy, or sandy-mud beaches, that is, in forms to which protectively colored carapaces are presumably of vital importance. Certain species, for example *Xanthodius sternberghii*, *X. stimpsoni* and *Ocypode gaudichaudii*, all showed remarkable individual and/or group adaptations to lighter or darker substrata, whether the general color of a beach was involved, or only that of a group of atypically colored pebbles. Whether these differences are genetic or somatic, individually fixed or adaptive, is unknown. Unfortunately, genetic study is not yet practicable, because of lack of successful rearing technique. However, even the simplest experiments concerning the extent of individual ability to change color would be very worthwhile.

Other forms of color variation are geo-

graphical and/or ecological, and further observations are greatly needed. One example is discussed under *Grapsus* (p. 84), and others in the discussions of *Uca princeps* and *U. beebei* (Crane, 1944, p. 166). Sometimes geographic variation in color is indicated in the rare observations of young stages from different localities. For example, the juvenile color patterns of *Carpilodes cinctimanus*, *Actaea dorii*, *Actaea sulcata*, *Cycloxanthops vittatus* and *Ozius perulatus* appear to differ on the mainland and in the Galápagos. (cf. color descriptions of these species in the present paper with those of Garth, 1946.1).

The field of epigamic colors is practically unexplored in crabs, except for some observations on *Uca*. Especially needed are ingenious, basic experiments on color vision and on the tendency of certain crabs in breeding condition to develop white pigment (see Crane, 1944).

5. DAILY ACTIVITY CYCLE: This field was scarcely touched during the expeditions since opportunities for night observations were few. The following divisions, however, were well established.

Diurnal: *Grapsus grapsus*; *Ocypode gaudichaudii*; most species of *Uca*?

Probably diurnal: *Xanthodius sternberghii*.

Diurnal and nocturnal: *Eriphia squamata* (more active at night); *Menippe obtusata*; *Pachygrapsus transversus* (more active during daylight).

Nocturnal: *Geograpsus lividus*; *Ocypode occidentalis*.

6. FOOD: The *Zaca* observations on feeding and stomach contents may be summarized as follows:

Vegetarians: *Daira americana*; *Xanthodius sternberghii*; *Pachygrapsus transversus*.

Predominantly vegetarians: *Grapsus grapsus*.

Carnivores and scavengers: *Menippe obtusata*; *Domacia hispida*; *Trapezia cymodeca*; *ferruginea*; *Trapezia digitalis*; *Geograpsus lividus*; *Ocypode occidentalis*.

Omnivores: *Eriphia squamata*; *Eriphiae hispida*; *Eurypanopeus planus*.

Feeders on microorganisms and organic detritus sifted from sand and mud: *Goniopsis pulchra*; *Ocypode gaudichaudii*; *Uca* spp. (the latter are sometimes also scavengers).

In regard to the general feeding habits of these intertidal species, the rather obvious statement may be made that all spider crabs and most xanthids, including naturally all *Pocillopora* inhabitants, feed when underwater, while the grapsids and ocypod-

<sup>2</sup> Martin D. Burkenroad in a forthcoming paper reports on the nocturnal, as well as diurnal, activity of an east coast *Uca*; all members of the genus must now be rechecked with his most interesting observations in mind.



lids are typically feeders in the air. However, observation will certainly draw finer distinctions. For example, although *Pachygrapsus transversus*, which frequently crawls around in tidepools, follows the grapsid custom and seems never to feed under water, *Sesarma* and other mud-livers in the family often eat when actually submerged in tidal puddles; this is also true occasionally of *Uca*. Again, *Eriphia squamata* feeds with apparently equal frequency both above and beneath the surface, being in this respect perfectly amphibious.

In the few observations that have been made, all species with spooned chelae are predominantly eaters either of close-growing rock algae, or of organic detritus in sand and mud. The species so far observed feeding in these fashions are *Xanthodius sternberghii*, *Pachygrapsus transversus*, *Grapsus grapsus*, *Ocypode gaudichaudii*, and the various species of *Uca*. The usefulness of the spoon adaptation is obvious. An exception is *Eriphides hispida*, which is probably chiefly carnivorous, although the minor chela is strongly spooned.

7. SOCIAL BEHAVIOR. The fields of gregariousness, territoriality, aggression and display are virtually untouched in these Pacific crabs, save for a beginning in *Uca* (Crane, 1941), and few observations have been made anywhere in the world. The following disconnected notes indicate the possibilities of crab-study as a focus for work on these general problems.

It was noted on the *Zaca* that, as in other animal groups, those crabs which are predominantly vegetarian or feeders on micro-organic food live in larger groups than predacious forms: for example, *Grapsus grapsus*, *Pachygrapsus transversus*, *Goniopsis pulchra*, both species of *Ocypode* and most *Uca* contrast with the solitary, carnivorous *Menippe obtusa* and, probably, *Eriphides hispida*.

Unlike *Uca*, *Goniopsis* shows little sense of territoriality, although both live comparable lives.

Sexual differences in aggression were noticed particularly in *Xanthodius sternberghii* and *Eurypanopeus planus*, as well as in *Uca*. In these forms, disturbed males are more aggressive than females, adopting the threat posture with chelipeds extended. In *Eriphia squamata*, on the other hand, both males and females threaten when actively disturbed, although the preferred reaction is to retreat, and their young never threaten.

There is evidence that in *Eurypanopeus planus* and *Trapezia cymodoce ferruginea* the sexes remain paired while the eggs are being carried, or, possibly, new pairs are being formed at that time.

8. BREEDING SEASONS. The breeding records included in this paper show only the months during which eggs were found on specimens collected in the various countries. The sole conclusion that can be drawn at present is that the series of most species yielded ovigerous females between December and May, the months during which our collections were made. The actual length and extent of the breeding seasons for different species in single localities, their variation with latitude, and their relation to the rainy season remain unknown.

#### REFERENCES CITED.

BEEBE, W.

1924. Galapagos: World's End. G. P. Putnam's Sons.

1938. Eastern Pacific Expeditions of the New York Zoological Society, XIV. Introduction, itinerary, list of stations, nets and dredges of the Eastern Pacific Zaca Expedition, 1937-1938. *Zoologica*, vol. 23, no. 14.

1942. Book of Bays. Harcourt Brace & Co.

BELL, T.

1835. Some Accounts of the Crustacea of the Coasts of South America, with Descriptions of new Genera and Species, founded principally on the collections obtained by Mr. Cuming and Mr. Miller. *Proc. Zool. Soc. London*, vol. 3, pp. 169-173.

BOONE, L.

1927. The Littoral Crustacean Fauna of the Galapagos Islands, Part I: Brachyura. *Zoologica*, vol. 8, no. 4, pp. 127-288.

1929. A collection of Brachyuran Crustacea from the Bay of Panama and the fresh waters of the Canal Zone. *Bull. Amer. Mus. Nat. Hist.*, vol. 58, no. 11, pp. 561-583.

1930. Scientific results of the cruises of the yachts "Eagle" and "Ara," 1921-1928, William K. Vanderbilt, Commanding. Crustacea: Stomatopoda and Brachyura. *Bull. Vanderbilt Marine Mus.*, vol. 2, pp. 5-228.

CRANE, J.

1937.1 The Templeton Crocker Expedition. III. Brachygnathous Crabs from the Gulf of California and the West Coast of Lower California. *Zoologica*, vol. 22, no. 3, pp. 47-78.

1937.2 The Templeton Crocker Expedition. VI. Oxystomatous Crabs from the Gulf of California and the West Coast of Lower California. *Zoologica*, vol. 22, no. 7, pp. 97-107.

1940. Eastern Pacific Expeditions of the New York Zoological Society, XVIII. On the Post-Embryonic Development of the Brachyuran Crabs of the Genus *Ocypode*. *Zoologica*, vol. 25, no. 6, pp. 65-82.



- 1941.1 Eastern Pacific Expeditions of the New York Zoological Society. XXVI. Crabs of the genus *Uca* from the West Coast of Central America. *Zoologica*, vol. 26, no. 3, pp. 145-208.
- 1941.2 Eastern Pacific Expeditions of the New York Zoological Society. XXIX. On the Growth and Ecology of Brachyuran Crabs of the Genus *Ocypode*. *Zoologica*, vol. 26, no. 29, pp. 297-310.
1943. Eastern Pacific Expeditions of the New York Zoological Society. XXXI. *Uca schmitti*, a new species of Brachyuran Crab from the West Coast of Central America. *Zoologica*, vol. 28, no. 6, pp. 31-32.
1944. On the color changes of fiddler crabs (Genus *Uca*) in the field. *Zoologica*, vol. 29, no. 3, pp. 161-168.
- EYDOUX, F. & L. F. A. SOULEYET.
1842. Voyage autour du monde exécuté pendant les années 1836 et 1837 sur la corvette "la Bonite" commandée par M. Vaillant. Tome 1, pt. 2.
- FINNEGAN, S.
1931. Report on the Brachyura Collected in Central America, the Gorgona and Galapagos Islands, by Dr. Crossland on the "St. George" Expedition to the Pacific, 1924-25. *Journ. Linn. Soc. London, Zool.*, vol. 37, no. 255, pp. 607-673.
- GARTH, J. S.
1940. Some New Species of Brachyuran Crabs from Mexico and the Central and South American Mainland. *Allan Hancock Pac. Exped.*, vol. 5, no. 3, pp. 53-95.
- 1946.1 Littoral Brachyuran Fauna of the Galapagos Archipelago. *Allan Hancock Pacific Exped.*, vol. 5, no. 10, pp. 341-522.
- 1946.2 Distribution Studies of Galapagos Brachyura. *Allan Hancock Pacific Exped.*, vol. 5, no. 11, pp. 603-638, charts 1-10.
- GIBBES, L. R.
1850. On the Carcinological Collections of the United States and an Enumeration of the Species contained in them, with Notes on the most remarkable, and Descriptions of new Species. *Proc. Amer. Assoc. Adv. Sci.*, vol. 3, pp. 167-201.
- GLASSELL, S. A.
1934. Some Corrections Needed in Recent Carcinological Literature. *Trans. San Diego Soc. Nat. Hist.*, vol. 7, no. 38, pp. 453-454.
1935. New or Little-Known Crabs from the Pacific Coast of Northern Mexico. *Trans. San Diego Soc. Nat. Hist.*, vol. 8, no. 14, pp. 91-106.
1936. The Templeton Crocker Expeditions. I. Six New Brachyuran Crabs from the Gulf of California. *Zoologica*, vol. 21, no. 17, pp. 213-218.
1940. In J. S. Garth, Some New Species of Brachyuran Crabs from Mexico and the Central and South American Mainland. *Allan Hancock Pac. Exped.*, vol. 5, no. 3, pp. 67-70.
- HULT, J.
1938. Crustacea Decapoda from the Galapagos Islands collected by Mr. Rolf Blomberg. *Arkiv för Zoologi, Stockholm*, Band 30A, no. 5, pp. 1-18.
- LATREILLE, P. A.
1825. Histoire Naturelle; Entomologie, ou histoire naturelle des Crustacés, des Arachnides, et des Insectes in; *Encyc. meth.*, vol. 10, pp. 1-832.
- LINNAEUS, C.
1758. *Systema Naturae*, ed. 10, vol. 1, pp. 1-823.
- LOCKINGTON, W. N.
1877. Remarks on the Crustacea of the West Coast of North America, with a Catalogue of the Species in the Museum of the California Academy of Sciences. *Proc. Calif. Acad. Sci.*, vol. 7, pt. 1, pp. 94-108, 145-156.
- MACCAGNO, T.
1928. Crostacei Decapodi. Le specie del genere *Uca* conservate nel Regio Mus. Zool. Torino. *Boll. Mus. Zool. ed Anat. Comp. R. Univ. Torino*, vol. 41, Ser. 3, no. 11, pp. 1-52.
- MILNE EDWARDS, A.
- 1873-1880. Etudes sur les Xiphosures et les Crustacés de la Région Mexicaine. *Mission Scientifique au Mexique et dans l'Amerique Centrale*, Pt. 5, pp. 1-368.
- MILNE EDWARDS, H.
1834. Histoire Naturelle des Crustacés, vol. 1, pp. 1-468.
1837. Histoire Naturelle des Crustacés, vol. 2, pp. 1-532.
- MILNE EDWARDS, H., & H. LUCAS
1843. In d'Orbigny, Voyage dans l'Amerique Méridionale, vol. 6, pt. 1, pp. 1-39; atlas, vol. 9, 1847, pls. 1-17.
- NOBILI, G.
1901. Viaggio del Dr. Enrico Festa nella Repubblica dell' Ecuador e regione vicine. Decapodi e Stomatopodi. *Boll. Mus. Zool. Anat. Comp. Torino*, vol. 16, no. 415, pp. 1-58.
- PEARSE, A. S.
1936. Estuarine Animals at Beaufort, North Carolina. *Jour. Elisha Mitchell Scientific Soc.*, vol. 52, no. 2, pp. 174-222.
- PESTA, M.
1931. Ergebnisse der Österreichischen Biologischen Costa-Rica Expedition 1930. I. Teil. Crustacea Decapoda aus Costa-Rica. *Ann. Naturhist. Mus. Wien*, vol. 45, pp. 173-181.



RATHBUN, M. J.

1893. Scientific Results of Explorations by the U. S. Fish Commission Steamer "Albatross". XXIV. Descriptions of new Genera and Species of Crabs from the West Coast of North America and the Sandwich Islands. *Proc. U. S. Nat. Mus.*, vol. 16, pp. 223-260.
1898. The Brachyura collected by the U. S. Fish Commission Steamer "Albatross" on the Voyage from Norfolk, Virginia, to San Francisco, California, 1887-1888. *Proc. U. S. Nat. Mus.*, vol. 21, pp. 567-616.
1906. Descriptions of three new mangrove crabs from Costa Rica. *Washington, D. C. Proc. Biol. Soc.*, vol. 19, pp. 99-100.
1912. New decapod Crustaceans from Panama. *Washington, D. C. Smithsonian Inst. Misc. Collect.*, vol. 59, no. 13 (Pub. 2090), pp. 1-3.
1918. The Grapsoid Crabs of America. *Bull. U. S. Nat. Mus.*, No. 97, pp. 1-461.
1923. The Brachyuran Crabs collected by the U. S. Fisheries Steamer "Albatross" in 1911; chiefly on the west coast of Mexico. *Bull. Amer. Mus. Nat. Hist.*, New York, vol. 48, pp. 619-637.
1925. The Spider Crabs of America. *Bull. U. S. Nat. Mus.*, No. 129, pp. 1-613.
1930. The Cancroid Crabs of America of the Families Euryalidae, Portunidae, Atelocyclusidae, Cancridae, and Xanthidae. *Bull. U. S. Nat. Mus.*, No. 152, pp. 1-593.

SAUSSURE, H. DE

1853. Description de quelques Crustacés nouveaux de la côte occidentale du Mexique. *Rev. et Mag. de Zool.*, ser. 2, vol. 5, pp. 354-368.

SCHMITT, W. L.

1939. Decapod and other Crustacea collected

on the Presidential Cruise of 1938. *Smithsonian Misc. Col.*, vol. 98, no. 6, pp. 1-29.

SIVERTSEN, E.

1933. The Norwegian Zoological Expedition to the Galapagos Islands 1925, conducted by Alf Wollebaek. VII. Littoral Crustacea Decapoda from the Galapagos Islands. *Medd. Zool. Mus. Oslo*, no. 38, pp. 1-38.

SMITH, S. I.

1869. Notes on new or little-known Species of American Cancroid Crustacea. *Proc. Boston Soc. Nat. Hist.*, vol. 12, pp. 274-289.
1870. Notes on American Crustacea. No. 1. Ocypodoidea. *Tr. Conn. Ac.*, vol. 2, pp. 1-24, 113-176.

STIMPSON, W.

1859. Notes on American Crustacea. No. 1. *Ann. Lyc. Nat. Hist. New York*, 1859 (1862), vol. 7, pp. 49-93.
1860. 22. Notes on North American Crustacea in the Museum of the Smithsonian Institution. No. 2. *Ann. Lyc. Nat. Hist. New York*, vol. 7, pp. 49-118 (177-246).
1871. 6. Notes on North American Crustacea in the Museum of the Smithsonian Institution. No. 3. *Ann. Lyc. Nat. Hist. New York*, vol. 10, pp. 2-46.

WHITE, A.

1847. Descriptions of a new genus and five new species of Crustacea. In Jukes, Narrative of the Surveying Voyage of H.M.S. "Fly", commanded by Captain F. P. Blackwood, R. N. in Torres Strait, New Guinea, and other Islands of the Eastern Archipelago during the years 1842-1846. Vol. 2, Append. no. 8, pp. 335-338.



